UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE
Northwest Region
7600 Sand Point Way N.E., Bldg. 1
Seattle, WA 98115

April 17, 2001

Dear Interested Party:

I am writing to announce the availability of an important technical report entitled "Independent populations of chinook salmon in Puget Sound." This draft document was prepared by the Puget Sound Technical Recovery Team (TRT), an independent scientific body convened by the National Marine Fisheries Service (NMFS) to develop technical delisting criteria and guidance for salmon recovery planning in Puget Sound. The TRT is seeking a thorough technical review of this draft document and desires comments by May 15, 2001. This report is a significant step toward development of a recovery plan through the Shared Strategy for Puget Sound Salmon Recovery.

The Shared Strategy is a collaborative effort to develop a recovery plan for salmon in Puget Sound during the next two years. More information is available on the Shared Strategy web site at www.sharedstrategy.com At a January Shared Strategy workshop in Port Ludlow, NMFS committed to provide population identification information for chinook salmon when it was available. NMFS is pleased to fulfill that commitment today. A copy of the TRT's report is attached and an electronic copy is available on the NMFS - Northwest Fisheries Science Center web site at (http://www.nwfsc.noaa.gov/cbd/trt/).

The first action in the TRT's effort to develop delisting criteria for Puget Sound chinook was to identify the independent populations of salmon throughout the Evolutionarily Significant Unit (ESU). As the document describes, the TRT identified 21 geographically distinct populations representing the primary historical spawning areas of chinook in Puget Sound. Throughout the summer and fall of this year, the TRT will complete additional technical analyses on the abundance, diversity, and spatial structure of these populations and the habitats that support them. The TRT will identify population-specific criteria for sustainability, identify multiple scenarios for population characteristics which would, if fulfilled, achieve recovery of the ESU as a whole, and evaluate the types of actions that would result in the greatest benefit to the populations. The next step in the Shared Strategy will be a document that defines interim recovery goals for chinook populations in Puget Sound. The TRT, NMFS, Tribes and State anticipate release of the interim goals document in June.

It is important that people reviewing the population identification paper understand the implications of this technical analysis and the TRT's continued scientific work. In short, the report identifies multiple independent spawning populations of chinook that will be the basis for an ESU-wide recovery strategy. According to the TRT, there are streams within Puget Sound that currently are not assigned to a population. Their unassigned status reflects incomplete information or analyses. Another subset of these unassigned streams likely will remain outside the boundaries of independent populations even after the TRT completes its population identification work.

Chinook born in Puget Sound use a number of freshwater, estuarine, nearshore, and marine habitats during their life cycle. Only a portion of these freshwater habitats will be included within the geographic boundaries identified by the TRT. In identifying population boundaries, the TRT's intent was to include only primary spawning habitats of the fish rather than including all the habitats that are important throughout their life cycle. This document **does not** describe the relative importance to recovery of either populations or the habitats that support them. The relative importance of particular populations and habitats to the recovery potential of chinook in Puget Sound will be addressed in future TRT analyses.

The TRT's population identification report does not evaluate the importance of fishery management or habitat quality and quantity to chinook recovery. Accordingly, NMFS wants to underscore the importance of fishery management and habitat conservation efforts in watersheds throughout the ESU. Based on the current status of chinook in Puget Sound, NMFS believes it is important to continue ESU-wide protection and restoration activities while the TRT, the state, and tribal governments develop recovery goals. NMFS will continue to work with the Shared Strategy to identify opportunities for conservation and support those efforts.

In the months ahead, NMFS will work in partnership with Shared Strategy members to develop and implement a recovery plan for listed chinook and other species in Puget Sound. The TRT will complete assessments of population sustainability and identification of ESU-wide recovery scenarios during the summer and fall of this year. We will provide this information to you as it becomes available and will look to the Shared Strategy to assist us in conveying the information to interested parties in watersheds across the Sound, and enlisting their participation and support in salmon recovery.

Sincerely,

Donna Darm
Acting Regional Administrator

UNITED STATES DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
NATIONAL MARINE FISHERIES SERVICE

Northwest Fisheries Science Center
2725 Montlake Blvd. E
Seattle, WA 98112

17 April, 2001

Dear interested party,

Enclosed please find a draft document for your review, entitled, "Independent populations of chinook salmon in Puget Sound." This draft is a product of the Puget Sound Technical Recovery Team (TRT), which was convened by NMFS in April, 2000 to develop delisting criteria and provide technical guidance in recovery planning for the listed Evolutionarily Significant Units (ESUs) of salmon in the Puget Sound region (i.e., Puget Sound chinook salmon, Hood Canal summer chum salmon, and Lake Ozette sockeye salmon.) An electronic copy of this document and more information on the TRT and recovery planning for Pacific anadromous salmon can be found on the NMFS-NWFSC web site (http://www.nwfsc.noaa.gov/cbd/trt/).

As we explain in the enclosed document, population identification is an important first step the TRT is taking in developing delisting criteria for ESUs. These populations are the independent groups of fish whose historical and present condition will be characterized. In subsequent documents, the TRT will present results estimating viability criteria for each population; or the number, productivity, diversity and spatial distribution of fish needed for a population to be naturally self-sustaining. The final step the TRT will take in developing ESU delisting criteria is to generate scenarios by which population characteristics can add up to a self-sustaining ESU. In short, the independent populations identified in this document will become the re-building blocks for designing a strategy to recover the ESU as a whole.

Chinook salmon from some Puget Sound streams are not presently assigned to an independent population. Some of these fish eventually may be assigned to a population if better information becomes available. Streams that remain unassigned are those that were most likely not primary spawning areas for chinook, which is the basis for our delineation of geographic boundaries for populations. Habitats and fish outside of independent population boundaries may be important for ESU viability.

This document does not evaluate the relative importance of these independent populations or habitats to ESU recovery. The TRT will report analyses addressing such issues at a later date, along with population identification and delisting criteria for Hood Canal summer chum salmon and Lake Ozette sockeye salmon. The recovery goals for the Puget Sound chinook ESU are scheduled to be published in a draft recovery plan in December, 2003. The process by which technical and policy considerations are combined to complete a recovery plan is being coordinated by a regional forum called the Shared Strategy (http://www.sharedsalmonstrategy.org/).

We solicit your input on all aspects of this draft technical report. In particular, we would like feedback on the criteria we have chosen to identify population boundaries. In addition, we know that we have probably missed biological details specific to individual watersheds--any information that you have that can further inform our population delineations would be greatly appreciated. We value your help in making population determinations as biologically accurate as possible. As with many scientific exercises, there is significant uncertainty in some of our conclusions. This is due mainly to the limited information available on which to make the determinations. If information that might alter our conclusions becomes available, we will re-visit population structure decisions made to date. Additional details of data types, supporting information, and analyses underlying population determinations in this draft are contained in a draft Appendix that will be posted on the NMFS-NWFSC recovery planning web site (http://www.nwfsc.noaa.gov/cbd/trt/) by April 20, 2001.

Our timetable for review of comments from you is short—we plan to release a final draft of this document and the Appendix in early summer, 2001, and so we ask that your comments be sent to us by **May 15, 2001**. Please send written comments to Mary Ruckelshaus at NMFS-NWFSC (email: mary.ruckelshaus@noaa.gov or by postal mail.)

Sincerely,

The Puget Sound TRT
Mary Ruckelshaus, chair
Ken Currens
Jim Doyle
Bob Fuerstenberg
Bill Graeber
Kit Rawson
Norma Jean Sands
Jim Scott

Independent populations of chinook salmon in Puget Sound

Puget Sound TRT Public review draft

11 April, 2001

The Puget Sound TRT: K. Currens, Northwest Indian Fisheries Commission; J. Doyle, U. S. Forest Service; R. Fuerstenberg, King Co. DNR; W. Graeber, Washington DNR; K. Rawson, Tulalip Tribes; M. Ruckelshaus and N. Sands, NMFS –Northwest Fisheries Science Center; and J. Scott, Washington Dept. of Fish and Wildlife.

Additional contributors to this report: E. Buhle, L. Holsinger, and T. Beechie, NMFS-NWFSC; A. Marshall and C. Busack, WDFW.

Note: An electronic copy of this document and the accompanying technical Appendix are available in PDF format on the NMFS-NWFSC web site at (http://www.nwfsc.noaa.gov/cbd/trt/).

(The Appendix will be posted April 20, 2001.)

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INTRODUCTION

The first task of the Puget Sound Technical Recovery Team (TRT) in developing recovery plans is to delineate independent populations within each of the 3 Evolutionarily Significant Units (ESUs) assigned to us. Understanding the size and spatial extent of populations is critical for viability analyses that are a necessary step in recovery planning and conservation assessments for any species. This report describes the delineation of populations for the Puget Sound Chinook ESU. Future reports will cover the Hood Canal summer chum and Lake Ozette sockeye ESUs. The populations we identify represent what we believe to be the historical populations of chinook within the Puget Sound ESU. Anecdotal evidence suggests that there were probably additional populations of chinook within the ESU that have since gone extinct (summarized in Myers et al. 1998). Moreover, due to considerable manipulation of watersheds over the long history of human occupation in the region, it is likely that some historic population structure has been lost or substantially modified from pre-management conditions. The populations we identify in this document are the independent groups of fish whose historical and present status will be characterized and for which viability will be assessed. For each population, we will in future documents describe numbers and productivity of salmon, life history and phenotypic diversity, and spatial distribution of spawning and rearing groups. In the ultimate recovery goals expressed for the Puget Sound ESU, the populations identified in this document will be those considered when answering the question: "What are necessary population characteristics that will add up to persistence of the ESU?"

In the *Salmon and Steelhead Stock Inventory* (SASSI, WDF et al. 1993), Washington state and tribal co-managers delineated individual stocks of Pacific salmon based on geographical and temporal separation in spawning and distinct biological characteristics (e.g., population gene frequencies, fish size, age structure, etc.) The definition of a stock used in the SASSI determinations is essentially the same as one first put forward by Ricker (1972) and is equivalent to the definition of a population we use in this analysis (see below). Using some of the same indicators as SASSI plus additional or updated information, we applied a systematic analytical approach to delineating populations within the Puget Sound Chinook ESU.

Definition of a population used in this approach

The definition of a population that we use in this report is defined in the Viable Salmonid Population (VSP) document (McElhany et al. 2000). See the VSP document for further discussion and elaboration of ideas and terms used here. The following section is a portion of the VSP document explaining the definition we use.

> A viable salmonid population (VSP) is an independent population of any Pacific salmonid (genus Oncorhynchus) that has a negligible risk of extinction over a 100-year time frame due to threats from demographic variation (random or directional), local environmental variation, or threats to genetic diversity (random or directional).
>
> In the VSP context, NMFS defines an independent population much along the lines of Ricker's (1972) definition of a "stock". That is, an

independent population is a group of fish of the same species that spawns in a particular lake or stream (or portion thereof) at a particular season and which, to a substantial degree, does not interbreed with fish from any other group spawning in a different place or in the same place at a different season. For our purposes, not interbreeding to a "substantial degree" means that two groups are considered to be independent populations if they are isolated to such an extent that exchanges of individuals among the populations do not substantially affect the population dynamics or extinction risk of the independent populations over a 100-year time frame. The exact level of reproductive isolation that is required for a population to have substantially independent dynamics is not well understood, but some theoretical work suggests that substantial independence will occur when the proportion of a population that consists of migrants is less than about 10% (Hastings 1993). Thus independent populations are units for which it is biologically meaningful to examine extinction risks that derive from intrinsic factors such as demographic, genetic, or local environmental stochasticity.

Structure below and above population level

A population is described as a group of fish that is reproductively isolated "to a substantial degree." As a criterion for defining groups of fish, the degree of reproductive isolation is a relative measure, however, and can vary continuously from the level of pairs of fish to the degree of reproductive isolation separating species. The "population" defined here is not, therefore, the only biologically logical grouping that can be constructed. Below the level of the population, for example, there will often be groups of fish that are to some degree reproductively isolated from other groups of fish within the population, but are not sufficiently isolated to be considered independent by the criteria adopted here. These groups of fish are referred to as "subpopulations." As will be described, the existence and interaction of subpopulations can have important consequences for characterizing a VSP, and population spatial structure is proposed as one of four key parameters for evaluating the status of a population.

Just as there may be substructuring within a population, there may be structure above the level of a population. This is explicitly recognized in the designation of an ESU. An ESU may contain multiple populations that are connected by some small degree of migration. Thus organisms can be grouped in a hierarchical system where we define the levels of individual, subpopulation, population, ESU and finally species. Other hierarchical systems with more or fewer levels could be constructed. Though reproductive isolation forms a continuum, it is probably not a smooth continuum, and there exists a biological basis for designating a hierarchy of subpopulations, populations and ESUs.

Independent populations will generally (but not always) be smaller than a whole ESU, and will generally inhabit geographic ranges on the scale of whole river basins or major sub-basins that are relatively isolated from outside migration.

CONCEPTUAL APPROACH TO IDENTIFYING POPULATIONS

We interpret the definition of a population cited above to mean that the populations of chinook we describe in this document are at least 100 years old. In some cases, the fish presently contained within the geographic boundaries of these historical populations do not represent the genetic legacy of the fish present historically (e.g., if the fish are an introduced hatchery stock). Our aim here is to identify geographic boundaries of historical populations of chinook. Subsequent analyses will determine the origin of fish contained in these populations and what their role should be in recovery.

Indicators of population structure

The definitive information needed to identify populations is inter-group migration rates and the demographic consequences of those migration rates. In practice, information on straying of salmon between streams is rarely available. Our approach in identifying population structure is to use diverse sources of information that are proxies for understanding the degree of reproductive isolation between groups of fish. Each type of information contributes to our understanding of population boundaries, but none alone provides us with much confidence in our answer. Below, we briefly outline the different sources of information one could use in identifying populations of salmon. They are discussed in order of the strength of inference we believe it is possible to make about population structure from each indicator, beginning with relatively high inference that can be made with geographic indicators. Depending on the particular data quality (see *Data quality*) and the genetic and demographic history of salmon in different regions, the usefulness of these indicators in any one area varies.

1. **Geography**. The boundaries of a salmon population will be defined, in part, by the spatial distribution of its spawning habitat. Physical features such as a river basin's topographical and hydrological characteristics dictate to a large degree where and when salmon can spawn and delimit the spatial area over which a single group of fish can be expected to interact. Geographic constraints on population boundaries (such as distance between streams) can provide a useful starting point from which to look more closely at the attributes of groups of fish within circumscribed geographic areas, but will not generally support strong inferences at finer scales (e.g., distinguishing separate populations within a small river basin.) In addition, biogeographic characteristics and historical connections between river basins on geological time scales can also be informative in defining population boundaries.

2. **Migration rates**. The extent to which adults move between sites will affect the degree of reproductive isolation, and therefore, demographic independence between sites. Straying estimates are the primary indicators available of the amount of connectivity between spawning aggregations. Stray rate estimates are particular to a group of fish and the season and streams in which they are made, thus they provide useful information about straying under current conditions. In contrast, it is not possible to obtain estimates of the magnitude of their variation over long time periods

(e.g., 100 years). Compared to mark-recapture and other direct estimates of straying, indirect estimates such as genetically based estimates of inter-group isolation can be used to estimate straying that has occurred between groups of fish, integrated over longer time periods than direct estimates.

3. **Genetic attributes**. Neutral genetic markers are useful in identifying salmon populations because they indicate the extent of reproductive isolation among groups. Neutral markers can be difficult to interpret because patterns may reflect hatchery practices or non-equilibrium conditions, and should be interpreted with caution. Adaptive genetic differences among groups of fish (as indicated by quantitative traits or molecular markers) are more difficult to document than discrete marker differences, but they offer good supporting evidence for distinct populations.

4. **Patterns of life history and phenotypic characteristics**. Technically, only those phenotypic traits based on underlying genetic variation (rather than environmentally induced variation) are informative in identifying populations (defined on the basis of reproductive isolation and demographic independence). Nevertheless, phenotypic variation can be used as a proxy for genetically based variation, and it also may indicate similarities in the selective environments experienced by salmon in different streams.

5. **Population dynamics**. Abundance data can be used to explore the degree to which demographic trajectories of two groups of fish are independent of one another. All else being equal, the less correlated time series of abundance are between two groups of fish, the less likely they are to be part of the same population. Complicating the interpretation of correlations in abundance between groups of fish is the potentially confounding influence of correlated environmental characteristics. When groups of fish that are in close proximity are not correlated in abundance over time, it is likely that they are not linked demographically. The reverse is not always the case—when correlations in abundance between groups of fish are detected, more work is needed to rule out confounding sources of correlation.

6. **Environmental and habitat characteristics**. The collective biotic and abiotic characteristics of occupied salmonid habitat help define a population because we expect that those ecological characteristics constitute the selective environment in which the salmon exist. The relative strength of inference for these characteristics is weak because we generally don't know which environmental variables influence the fitness function, or whether those effects will be observed at the population level. If different groups of salmon experience different selective environments and there is very little migration between those environments, we expect those groups' phenotypic characteristics to diverge.

Data quality

An important first step in analyzing and interpreting any of the population structure indicators above is to carefully screen the data and information for potential sources of error or bias. To minimize such error, we consulted with biologists familiar with adult and juvenile sampling methods and calculations used to expand from index

counts to total abundance estimates for each stream before data were used in analyses. Wherever possible (e.g., for calculating trends in abundance), index counts are used in lieu of expansions in order to minimize errors or bias due to spatial variation in expansion methods (e.g., Smith and Castle 1994). In cases where fish survey methods are unreliable or expansion methods are undocumented or inconsistent over time, data were not used in analyses. In many instances, counts of juveniles and adults include an unknown mixture of naturally produced fish and first generation hatchery fish. Abundance measures used in these analyses refer to estimates of the number of spawning adults.

Genetic data can be rendered uninformative for population structure considerations if a stream contains non-native, hatchery-origin fish that cannot be easily separated in a sample. Wherever possible, we use information from the history of stock transfers and broodstock origin to determine whether a genetic sample from a stream would be indicative of the genetic makeup of native fish. Even if the existing fish in a particular stream are not native, estimates of their genetic similarity to fish in other streams can be informative for determining migration estimates if the length of time the non-native stock has been present in the stream can be estimated.

Similar to potential problems cited above for fish count expansions, coded-wire tag expansion methods are notoriously variable in different streams and years. We consulted with biologists familiar with expansion methods in different areas to try and minimize error or bias introduced from variable expansion methods.

Evaluating similarity between groups

For each of the population structure indicators, the answer to whether a particular attribute in one group of fish is "similar" to that in another group must be addressed. In general, we believe that for conservation applications, it is most appropriate in constructing hypotheses to assume that any two groups of fish are separate unless the data indicate they should be combined into a single group. This approach errs on the side of conserving diversity that might otherwise be lost if a distinct group of fish is incorrectly lumped with a larger group. Since similarity is a relative term, it is incumbent upon those designing analytical approaches to explicitly decide for each population indicator what criteria will be used to determine how similarity relates to demographic independence. This is not a simple exercise—for example, with advances in genetic marker development, individual fish routinely can be determined to be statistically significantly different from one another. For some attributes, statistical significance is not necessarily an appropriate test for whether two groups of fish belong in the same population. The goal of a similarity "test" in the context of population identification is to distinguish **biologically** significant differences among groups of fish for each attribute. The challenge for those interpreting the results of statistical analyses is to decide the biological significance of the clusters, and how statistical significance can be used to help inform the decision about population independence. For example, information from studies of the adaptive significance of phenotypic trait variation can be helpful in determining the magnitude of differences in phenotypic traits that might be associated with different populations. Similarly, determining whether migration rates are "high" enough between groups of fish to consider them to be in the same population also is a relative question. Population genetic theory can be instrumental in helping to estimate the genetic consequences of particular migration rates.

Barring information such as the adaptive significance of phenotypic information, we believe that statistical significance is informative for ruling out instances where groups of fish should not be considered independent. Two groups of fish should not be considered to be independent populations if there are no statistically significant differences in attributes between the groups (unless the data are suspect—e.g., if the data are scarce or likely to be affected by the presence of non-local hatchery fish). The converse is not true—groups of fish can be combined into a single population even if there are statistically significant differences between the groups in some attributes. In such cases, the power of the test may be high enough to detect significant substructuring within a population, but the differences are not deemed large enough to indicate distinct populations. As emphasized earlier, it is important to remember that population structure is hierarchical in nature. Therefore, part of identifying populations of salmon involves describing the nested pattern of population structure (e.g., subpopulations, populations and possibly metapopulations).

The *Methods and Results* section that follows describes data analyses we conducted for those indicators that turned out to be useful in our population structure decisions (i.e., geography, genetics and some life history information). At the end of the section is a description of how we summarized analyses for these indicators and made population structure determinations. The remaining indicators did not produce results that were as useful for our population structure decisions. Results were relatively uninformative for various reasons, including unresolvable data quality problems, weak inference, and inconclusive results. The *Methods and Results* sections for the relatively uninformative indicators are presented in the *Appendix*. We present those results in the *Appendix* to complete the documentation of our analyses and to motivate further data collection that may render such information more useful in the future. The draft *Appendix* will be posted on the NMFS-NWFSC recovery planning web site (http://www.nwfsc.noaa.gov/cbd/trt/) by April 20, 2001.

METHODS AND RESULTS

Geographic distribution of Puget Sound chinook

The spatial distribution of primary spawning locations of chinook salmon in Puget Sound is depicted in Figure 1. These spawning distributions are for those of SASSI stocks identified by co-managers (WDF et al. 1993). The colors in the map distinguish presumed run-timing life history types: spring, summer, summer/fall and fall. There is little information on the location of rearing areas used by chinook juveniles, and of historical spawning distributions in most basins. Table 1 provides a list of streams from which we use data in this report and the river basins in which those streams occur.

The geographic distances (km) separating all spawning areas are presented in a matrix in Table 2. Distances were calculated as the shortest nautical distance separating each pair of spawning sampling sites, including the river distance plus the distance between river mouths where applicable. Distances were measured using GIS software

and a 1:250,000 scale map. Catchment area was calculated for Puget Sound streams containing chinook salmon populations using a Geographic Information System. Catchment area included the entire watershed from the river's mouth upstream to its headwaters. Exceptions are large watersheds, like the Skagit River, which have main channel splits as well as substantial contributing tributaries. In these cases, calculation of catchment area excluded portions of the watershed above major upstream confluences (e.g., the lower Skagit River includes the area from the mouth of the river to the confluence with the Sauk River) (Fig. 2).

Theoretically, a "minimum catchment area" could be defined that indicates the minimum watershed area needed to support a self-sustaining population of chinook. We are not able to define such a minimum area in this document because an independent assessment of population boundaries must first be made. The distribution of catchment sizes in major Puget Sound river basins varies by an order of magnitude (Fig. 2)—areas range from over 600,000 ha in the Skagit River Basin to just under 20,000 ha in the Duckabush River. Identifying the watershed area below which an independent population of chinook cannot be sustained requires that independent sources of information lead to population identification. In this document, the smallest watershed containing what we believe to be an independent population is the South Fork of the Nooksack River (47,700 ha). Whether watersheds smaller than that also can support independent populations is not possible to estimate with the information to date.

Direct observations of migration

Some direct observations of straying among Puget Sound chinook stocks were available. Most of these observations were based on releases and subsequent recoveries of hatchery chinook marked with coded-wire tags, available in a database maintained by the Pacific States Marine Fisheries Commission (RMPC 1997). We were not able to get good estimates of stray rates--the proportion of all fish in a tag group (or from a release site) that are recovered somewhere other than their tagging/release site-- because methods of estimating the total number of returning tagged fish vary among recovery locations and the geographic area sampled for strays is not appropriately selected. Furthermore, how well straying patterns of hatchery fish reflect those of wild chinook is not well known. Estimates of straying rates based on small-scale experimental studies were available in a few locations. Summary of information collected and results for this indicator are reported in the *Appendix*.

Genetic attributes

Methods

Characterization of genetic differences among stocks of Puget Sound chinook was provided by WDFW (A. Marshall and C. Busack, WDFW, pers. comm.). WDFW systematically samples chinook salmon from Puget Sound streams for genetic and life history characterizations, and they have developed an extensive database covering multiple brood years (1980-1996; Table 3). Twenty-nine polymorphic allozyme loci were used in genetic distance analyses for 33 groups of chinook sampled from Puget Sound streams. Only those sites for which there were at least 50 fish were included in the

UPGMA dendrogram, which depicts the Cavalli-Sforza and Edwards (1967) chord genetic distances separating each pair of sites. Multiple broodyears were combined within a site for this analysis because among-site variation is higher than genetic variation among broodyears within a site (A. Marshall, WDFW, pers. commun.). We examined the robustness of the patterns of genetic similarity by bootstrapping the genetic distance matrix over loci. We performed UPGMA cluster analysis on 1000 resampled gene frequency datasets and used the resulting dendrograms to construct a consensus tree. Bootstrapping analyses were conducted using the PHYLIP computer package (Felsenstein 1993).

The same samples included in the UPGMA analysis were also visualized using a multi-dimensional scaling (MDS) algorithm (Lessa 1990). For the MDS analysis, we conducted a principal coordinates analysis on the matrix of genetic distances, and used results as an initial configuration for multidimensional scaling. We used chord distances in cluster analyses (unweighted pair-group method, Sneath and Sokal 1973), and multidimensional scaling analyses using the BIOSYS-1 computer program (Swofford and Selander 1989) and the NTSYS-pc program (Rohlf 1994), respectively.

We used contingency table tests to ask whether observed allele distributions from different groups were drawn from the same underlying distribution (Weir 1996). Log-likelihood G-tests were used to test the null hypothesis that samples of alleles from two groups were randomly drawn from the same population.

In order to assess the spatial scale of genetic similarity, we examined the association between genetic distance and the geographic distance separating sampling sites. Geographic distances (as previously described) were calculated as the shortest nautical distance separating each pair of sampling sites, including the river distance plus the distance between river mouths, where needed. Distances were measured using GIS software and a 1:250,000 scale map. A one-tailed Mantel test with 2,000 bootstrap re-samples was used to test for a positive association between geographic and genetic distance matrices.

Population structure statistics were estimated from allozyme data using Weir and Cockerham's (1984) approach to estimating genetic differentiation among groups. ANOVA is used to partition the total genetic variation in a sample to that among and within groups. The genetic variation among groups is termed θ; a θ equal to 0 indicates that there is no significant difference between groups in genetic composition, and a θ equal to 1 indicates that the two groups have completely fixed genetic differences. From θ, an indirect estimate of gene flow (Nm) can be estimated (Slatkin 1985). Nm is the effective number of migrants per generation, and is estimated from θ as:

$$\theta = 1/(1 + 4Nm)$$

This approximation assumes an infinite island population genetic model and that the pattern of allele frequencies among populations is due to gene flow (instead of mutation, selection or random genetic drift, for example.) Extensive simulations have shown that the approximation of gene flow using this equation is robust to violations of the simplifying assumptions (Slatkin and Barton 1989). Pairwise estimates of θ were calculated between all groups within a watershed.

We also estimated effective population size (*Ne*) and time since divergence (*t*) from allozyme data to help in better understanding how migration and genetic drift might have contributed to observed genetic differences between groups. *Ne* estimates provide an indication of the likelihood that genetic drift in small populations has contributed to their genetic composition. *Ne* (and *Nb*, the effective number of breeders) has been estimated for a number of salmonid species (Waples 1990, Waples et al. 1993, QAR draft), resulting in *Nb/N* values for chinook salmon in the range of 0.3 – 0.4. We adjusted yearly census (*N*) values by the *Nb/N* ratio of 0.3 and computed the harmonic mean *Nb* for each group. We then computed $Ne = gNb$, where *g* is the mean age at spawning for each group. We computed pairwise *Ne* between all groups within a watershed by taking the harmonic mean of *Ne'*s for each group.

The time since divergence (*t*) can be estimated from θ and *Ne*, assuming that each group is completely isolated from one another (Weir 1996). Under this model, the two groups are assumed to have diverged from a common ancestral populations *t* generations ago and have not had any gene flow between them since divergence. This approximation also assumes discrete generations, random mating within groups, and selectively neutral genetic variation. Although Pacific salmonids do not have discrete generations, Waples (1990) has shown that this violation is not likely to greatly affect estimates of *t* over long time periods. In identifying populations, we are interested in asking whether divergence times are greater or less than 100 years. The estimate of *t*

from *Ne* and θ is:

$$t/2Ne = -\mathrm{Ln}(1 - \theta)$$

Results

Clusters of genetically similar chinook salmon in Puget Sound streams are generally consistent with the spatial configuration of the streams, especially in the northern Puget Sound region (Fig. 3A and B). Visualized in either two or three dimensions, there are 6 main clusters of chinook in Puget Sound: (1) Elwha River chinook (not shown in MDS plot), (2) early-returning chinook in the North Fork Nooksack River, (3) early-returning chinook in the South Fork Nooksack River, (4) chinook in the Skagit, Stillaguamish, and Snohomish River basins, (5) chinook in South Puget Sound and Hood Canal, and (6) White River early-run chinook salmon. In contrast to the genetic distinctions among chinook in different river basins in North Puget Sound, the resolution of the genetic data is poor in South Puget Sound and in Hood Canal because of the extensive presence of hatchery chinook. Therefore, for the purposes of identifying historical population structure, the genetic data are not very informative for South Puget Sound or Hood Canal regions. There are some genetic samples available from the Dungeness River (not shown in Figure 3). The number of chinook sampled from the Dungeness River recently has been increased to be considered a representative genetic sample (n > 50 fish) and results from preliminary analyses suggest that the Dungeness chinook are intermediate in their genetic composition between Puget Sound and Elwha River chinook (A. Marshall, WDFW, pers. comm.).

The boostrapped consensus tree depicted in Fig. 4 shows that there is good statistical support for some of the relatively deeper branches in the dendrogram. In

contrast, the specifics of genetic clustering within the Skagit and Stillaguamish River Basins and within the Skykomish River Basin are not well resolved.

Results from contingency tests among samples from different locations indicate that allele frequencies from many samples are significantly different from one another. The only pairs of samples whose contingency tests were not statistically significant were the Wallace-Skykomish, Wallace-Bridal Veil and Bridal Veil-Skykomish in the Snohomish River Basin and the Newaukum-Green samples. The significant G-test results among sites in the Skagit River Basin are different than those detected at the time the SASSI document was completed (WDF et al. 1993; B. Hayman, Skagit System Cooperative, pers. commun.).

Genetic divergence between stocks increases with geographic isolation (Fig. 5). A one-tailed Mantel test indicates significant positive association between genetic and geographic distance ($P < 0.001$). The relationship between genetic and geographic distance appears to be linear, with no obvious thresholds that might indicate the scale over which among-population gene flow occurs.

Genetic differentiation among all groups of chinook in Puget Sound is $\theta = 0.063$, corresponding to an estimated gene flow between groups equal to 3.7 effective migrants per generation (Table 4). Within major watersheds, θ ranged from 0.002 among sites sampled in southern Puget Sound to 0.031 among 6 stocks within the Skagit River Basin. In general, θ values among stocks within a river basin were less than 0.02. Exceptions occur in the Nooksack River, where genetic differentiation between the North and South Fork stocks is $\theta = 0.024$, and in the Stillaguamish, where θ between 2 stocks is = 0.051.

Estimates of *Ne* for groups of Puget Sound chinook varied from *Ne* = 101 for the fish in the North Fork Nooksack River to *Ne* = 7,971 for the fish in the upper Skagit River (mean *Ne* over all groups = 1,320 fish per generation; median *Ne* = 573). Estimates of *t* between groups of chinook ranged from less than 0 generations (for chinook in Bridal Veil Creek-Skykomish River and Bridal Veil Creek-Wallace River) to 324 generations since divergence for chinook in the lower Skagit and lower Sauk rivers (mean *t* over all pairwise comparisons = 77 generations; median *t* = 25). Pairwise estimates of *t* indicate that roughly half of the groups of chinook (12 out of 26) have been isolated for less than 100 years (assuming a 5 year generation time). As discussed later (see *Population structure decisions*), these low estimates of *t* are difficult to interpret—violation of assumptions in the model used to estimate *t* from *Ne* are likely to make the true value higher. On the other hand, high values of *t* are not likely to be misleading, so the pairwise comparisons with *t* estimates greater than 100 years are more reliable.

Patterns in life history characters

Methods

Similarities in life history or phenotypic characters were used as possible indicators of genetic relationships among chinook stocks. In addition, examining the spatial pattern of phenotypic variation (such as that exhibited by life history traits) can suggest differences among sites in environmental characteristics that could promote adaptive divergence of

fish. More detailed analyses are needed to determine the adaptive significance of phenotypic variation; in the context of this document, we consider life history trait variation to be informative for population identification in a qualitative way. Three life history characters–age (at downstream migration and spawning), age-specific length, and timing of spawning–were analyzed in detail. Only time of chinook spawning was informative for our population structure decisions, so summaries of the other life history data are provided in the *Appendix*.

The timing of chinook spawning was inferred from time series of spawner densities (fish/mile) in index surveys conducted annually throughout Puget Sound. The annual survey data for each index area were screened to include only years in which at least six surveys were conducted and the densities on the first and last survey dates were at most 20% of the maximum density for the year. These criteria were intended to select annual time series that provide a reasonable estimate of the shape of the timing curve, particularly the tails. The yearly data were standardized to remove interannual variation in abundance and averaged over all years to give an average relative density curve for each index area. From each curve we calculated a weighted mean date of spawning, using the daily average relative spawner densities as weights. The absolute value of the difference between the mean spawning dates was calculated for every pair of index areas, and this dissimilarity matrix was used in a UPGMA cluster analysis.

Results

Cluster analysis based on differences in mean spawning date indicates that there are at least three fairly distinct groups, corresponding roughly to early through late August, late August through mid-September, and mid-September through late October (Fig. 6). These breakpoints, however, are not obvious from inspection of the range of mean spawning dates (Fig. 7), which suggests a more continuous distribution of spawn timing. At a finer level, different index areas within a single SASSI stock are sometimes very similar in their spawn timing (e.g., Suiattle River tributaries), but not always. In general, although there is a latitudinal cline in timing with earlier spawning in more northerly basins, index areas within a SASSI stock are not consistently more similar in their spawn timing than areas in different stocks.

Spatial synchrony in spawner abundance

Examining the patterns of covariation in abundance between groups of fish can theoretically provide an indication of the degree to which the groups are linked by migration. Unfortunately, there is another reason why groups of fish might exhibit similar population dynamics—they may experience similar environmental conditions. It is not possible to tease apart these two potentially confounding sources of covariation without experimentation. For these reasons (and the unknown proportion of hatchery fish in many groups), the results from these analyses were only partly informative for population structure decisions. On the whole, the relationships among stocks suggested by correlations in abundance are not concordant with the pattern suggested by geography and genetic similarity, i.e., geographically proximate stocks do not consistently show stronger correlations in abundance than geographically distant stocks. The analytical

approach to quantifying correlations in abundance and results from these analyses are reported in the *Appendix*.

Habitat characteristics

Describing patterns of regional habitat characteristics can provide insights into the selective environment fish experience, and therefore illuminate a potential influence on population structure. These analyses are potentially most useful in areas where genetic, abundance and life history data are not informative. We explored differences in habitat characteristics thought to affect chinook vital rates: (1) the hydrological characteristics of rivers and streams, (2) water temperatures, (3) EPA ecoregions defined by a composite of habitat features, and (4) underlying geological types. Differences in habitat characteristics among streams in Puget Sound are apparent, but the biological significance of those differences to chinook is not known. The strength of inference from these results is relatively low, as expected, thus the analytical approaches and results from these analyses are reported in the *Appendix*.

Population structure decisions

The six different indicators of population structure that we used (geographical distribution, migration, genetic differences, life-history differences, spatial synchrony in spawner abundance, and environmental differences) have different theoretical and actual value for identifying independent populations. Recognizing these differences, we examined the data hierarchically to make decisions about population structure. Using a list of all spawning aggregations in the Puget Sound derived from information in SASSI (WDFW and WWTIT 1993; Table 5), we first examined the geographic distribution of spawners within Puget Sound and circumscribed the watersheds we considered to be the largest scale at which independent populations were likely to occur. In many cases in northern Puget Sound, these watersheds were those that had a single outlet to Puget Sound. In the southern Puget Sound and in Hood Canal, some watersheds draining directly to Puget Sound were combined into a larger geographic area for consideration. This broader scale lumping reflects the greater degree of uncertainty about historical population structure in southern Puget Sound and Hood Canal, where the historical distribution and abundance of native, naturally produced chinook salmon are not well understood. It also reflects our uncertainty about the minimum watershed area capable of supporting an independent population. Within each of these groups, we examined each possible pair of spawning groups for independence. To standardize population data across indicators, all of the information for each indicator was summarized in a distance matrix representing the pairwise differences in the data type between all groups within a watershed (see *Appendix*).

Within geographically defined areas, we first considered genetic data to infer independence of different spawning aggregations. Independence scores of 3-4 for the genetic indicators (see below) provide a fair degree of confidence in determining that the two groups are separate, independent populations. No further information was needed from the other 4 population indicators in those cases where genetic data clearly indicated population structure. In contrast, when independence scores for genetic indicators ranged from 1-2, the genetic evidence supports population independence, but the confidence in

that determination is relatively weaker. In such cases, we used life-history differences in time of spawning to infer any remaining undetected independent populations among the remaining spawning aggregations. Although inferences from the other indicators (migration, spatial synchrony in spawner abundance, and environmental differences) were too weak to identify independent populations, we used these differences as "weight of the evidence" for lending support to (or increasing our uncertainty in) populations identified with geographic, genetic, and life history information.

We conducted a variety of analyses for each indicator that informed our interpretation of "independence." Where appropriate, statistical significance of the differences between groups was presented. We combined the analyses for each indicator to arrive at an assessment of independence in two ways: 1) In one instance, we developed a quantitatively-based decision rule that combined the results of the analyses for that indicator to arrive at a decision of independence or not. 2) Where this was not possible, we relied on the collective judgment of individuals who reviewed the quantitative data we summarized.

In each case, we assigned an independence score to each pair of sites within a watershed ranging from –4 (groups are part of the same population) to +4 (groups are independent populations). Scores ranging between –4 and +4 indicated the level of certainty in the decision about two groups being independent or part of the same population. This measure of certainty was based on two factors: the degree of difference indicated by the data itself, and the level of confidence the scorer had in those data. For example, a "0" indicated that there was either intermediate differentiation between the groups or that the population structure of the groups was not clear from the available information. Any positive score indicated that the evidence suggested that the two groups were independent populations. Similarly, scores less than 0 indicated that the two groups were part of the same population. For each indicator, we summarized the independence between each pair of sites as the median independence score across scorers (with 6-10 scorers per indicator) and the distribution of independence scores among scorers.

Genetic indicators

Ten professional geneticists from WDFW, NWIFC, and NMFS provided scores of independence based on the same set of analyses (Table 6). These analyses were 1) pairwise *P*-values from log likelihood ratio tests (G-tests) for significant differences in allele frequencies, 2) pairwise Cavalli-Sforza and Edwards genetic distances 3) a dendrogram and multidimensional scaling of similarities of Puget Sound chinook salmon based on Cavalli-Sforza and Edwards genetic distance, 4) pairwise Nei's genetic distances, 5) dendrogram of similarities of Puget Sound chinook salmon based on Nei's genetic distance, 6) pairwise estimates of θ, a measure of genetic differentiation between groups, 7) pairwise estimates of migrants per generation (*Nm*), and 8) pairwise estimates of how long populations had been independent (*t*, time since divergence). Analysis of the scoring indicated that *P*-values from G-tests, estimates of θ, and genetic distances were most influential in assessing independence. The group felt that if two groups of fish are not statistically significantly different from one another, it is not possible to consider them to be in two different populations. Conversely, it is possible that a single population could contain two subpopulations that are statistically significantly different

from one another in one or more genetic metrics. The geneticists also relied on estimates of time since divergence, because any bias in the estimates would tend to under estimate the time since divergence. Most scorers indicated that their scores closer to 0 indicated that the data were not clear, rather than intermediate degrees of independence.

Life history indicators

We ranked independence using a decision rule that related the degree of potential reproductive overlap (*P*) based on spawn timing to empirical evidence of reproductive isolation among sympatric populations. We scored groups as independent if $P < 0.01$, likely to be independent if $P < 0.100$, or unsure because of insufficient information if $P > 0.100$. This approach assumes that the degree of temporal overlap between spawning groups is a good estimate of reproductive independence (i.e., spatial distances separating groups and behavioral isolating mechanisms are not included in this estimate). Values of *P* from sympatric groups of winter and summer steelhead and summer and fall chum (Leider et al. 1984 and J. Haymes, WDFW, pers. commun.) were used to set threshold values that corresponded to different levels of confidence that the populations were independent (see *Appendix*).

Migration indicators

Estimates of straying from coded-wire tag groups were the only direct indicators of migration that are available. These data were not designed to address this question. Consequently, estimates were only mildly informative. Nevertheless, a matrix of straying estimates and dispersal curves generated from the CWT database (see *Appendix*) were helpful in identifying where straying has occurred between sites, and the distances over which fish traveled to stray.

Population dynamics indicators

Correlations in the time series of abundance were the only information available for chinook salmon. Because of the potentially confounding effects of correlated environmental conditions, these analyses were only mildly informative.

Habitat indicators

The most informative habitat information for identifying population structure that we examined was the correlation in flow from unregulated gages in Puget Sound rivers. Correlations in flow between those gages in close proximity to spawning aggregations were used to score similarity between sites in flow regime. Other habitat-related characteristics such as temperature during incubation, geological characteristics, and EPA ecoregions provided some corroborative information. We did not use this indicator to identify independent populations, but it did offer support for (or added uncertainty to) conclusions based on the three primary indica

CONCLUSIONS

The following section lists and describes the demographically independent populations we have defined for chinook salmon in Puget Sound (Table 7, Fig. 8). We have omitted classic "run timing" labels from population names to avoid false precision in delineating the life history characteristics of fish in these populations. In all cases, the populations we define are meant to represent the native fish that spawned and reared in these streams under historical conditions. As stated earlier, in some watersheds, the fish currently present do not represent those that were there historically. The origin of fish in populations we identify and their potential roles in recovery of the ESU will be determined in subsequent documents. The narratives following the populations briefly summarize the data and information we have been able to assemble to date.

Chinook spawning naturally that are not assigned to an independent population

There are chinook salmon spawning naturally in Puget Sound streams that are not presently assigned to an independent population. The major spawning aggregations of chinook in Puget Sound are listed in Table 5 (WDF et al. 1993). There are two main reasons why naturally spawning chinook may not have been assigned to a population. First, spawning adults are known to occur intermittently in certain streams—spawning in groups of tens to hundreds of fish in some years and none in others. A plausible biological explanation for intermittent occurrence of chinook in some streams is that those adults are part of a larger independent population that uses some spawning habitats only during years of high abundance or favorable habitat conditions. The streams that intermittently harbor spawning adults could contain fish from more than one independent population—the locations of the streams relative to the primary spawning areas of independent populations dictates how many populations might contribute fish to these "spillover" spawning areas. Second, it is possible that some streams presently containing chinook never supported naturally spawning chinook historically. In many of these instances, the origin of the naturally spawning chinook currently present is most likely due to hatchery production. Some streams may therefore contain chinook solely because of the presence of a hatchery, and they would not have represented historical chinook spawning habitat. As more information becomes available, it is possible that chinook in some intermittently used streams can be clearly associated with one or more populations, and their assignment will change to reflect their association with a particular population.

It is important to remind the reader that **the geographic boundaries of independent populations that we define in this document do not include all of the habitats that may be important to population viability or ESU recovery**. As stated earlier, we define populations in this document to include those areas that encompass the primary spawning habitats of chinook populations in Puget Sound. Identification of habitats used throughout the life cycle and their potential importance to recovery—including those used occasionally by spawning adults—must be addressed throughout the Puget Sound region. For example, habitats used by juveniles for freshwater, estuarine and nearshore rearing and foraging typically will not be included in the geographic boundaries of independent populations we identify in this document. That is not to say that we think those habitats are unimportant to recovery—many are likely to be critical to

the viability of the ESU, as discussed in detail in the Viable Salmonid Populations document (McElhany et al. 2000). The challenge for forthcoming analyses conducted by the TRT and others is to identify which habitats are the most important to protect or restore to ensure the viability of populations and the ESU. An important step in conducting these analyses is identifying which habitats fish occupy throughout their life history, and the population origins of fish in particular areas. As such information becomes available for chinook in Puget Sound, the geographic boundaries of populations we identify in this document can be modified.

Demographically independent populations of chinook salmon in Puget Sound

Nooksack River Basin

Chinook in the Nooksack River Basin are distinctive from chinook in the rest of Puget Sound in their genetic attributes, life history and habitat characteristics. Although some chinook from the Nooksack Basin (Kendall Creek hatchery) stray into other Puget Sound Basins, the low numbers observed probably do not have a significant effect on the demographic dynamics of the groups of fish in donor or receiving streams. The discussion below focuses on the evidence pertaining to the population structure of chinook salmon within the Nooksack River Basin.

1. **North Fork Nooksack River**
2. **South Fork Nooksack River**

Summary of information used in population structure decisions. The early-returning chinook salmon in the North and South Forks of the Nooksack river are in two demographically independent populations. Geographically, the primary spawning locations in the two streams are separated by almost 10 kilometers. The genetic independence score was 3 (Table 6), indicating strong support for separating these groups into two independent populations. Genetic data suggest that fish from the North and South forks of the Nooksack River are very distinctive. Indeed, the Cavalli-Sforza Edwards chord distance separating fish from the two forks of the Nooksack River is the second largest of any other joins in the dendrogram for the whole Puget Sound region (Fig. 3). In addition, the high θ value and significant p-value for G-tests support the conclusion that the two stocks in the Nooksack are independent populations. Chinook in the North and South forks of the Nooksack River are considered to be of natural origin, and the South Fork stock is thought to have little hatchery influence in spawning escapements (WDF et al. 1993, Myers et al. 1998). Marshall et al. (1995) consider the chinook in the two Nooksack forks to be separate Genetic Diversity Units (GDUs), based on genetic differences, geographic distribution and life history. Peak spawn timing is substantially different between groups of fish from the two Forks (Fig. 6)—confirming Marshall et al.'s results. Chinook in the South Fork spawn later on average and over a longer period of time than those in the North Fork (Fig. 7).

Summary of additional information. Coded wire tag recoveries (n = 10 fish from 1984 to 1992) indicate that straying between the two Forks is very low (Marshall et al. 1995). Coded wire tag data from 1973-1997 reported by PSMFC indicate that some

straying from the Kendall Creek Hatchery (North Fork Nooksack) and Skookum Creek (South Fork) to the other forks has occurred, although quantitative estimates of stray rates could not be made.

Age distributions of spawning fish from the two Forks are very different—more chinook from the South Fork tend to spawn as 5-year olds. In addition, the South Fork Nooksack chinook are slightly larger at a given age than the North Fork chinook, but the two groups cluster tightly when comparing length-at-age for all Puget Sound stocks. There are slight differences in marine and Puget Sound distributions of chinook from the North and South Forks of the Nooksack, according to coded wire tag data (Marshall et al. 1995). In addition, Marshall et al. (1995) reported that, based on analyses of scales of spawning adults, there is a greater proportion of smolts migrating as subyearlings in the North Fork than in the South Fork (95% of natural-origin adults returning to spawn in North Fork migrated as subyearlings vs. 33% in South Fork).

At the time we conducted these analyses, we did not have expanded abundance data from the North Fork Nooksack, so those fish were not included in the population synchrony analyses. Chinook abundance over time in the South Fork Nooksack is not correlated with any other groups of fish in Puget Sound (see *Appendix*).

Habitat differences between the North and South Forks of the Nooksack River based on hydrograph information are relatively subtle. The two forks do have different hydrographs—the North Fork is predominantly snowmelt-dominated and the South Fork is mixed rain and snowmelt- dominated. Furthermore, the hydroregions the two streams occur in are somewhat different—the North Fork drains primarily low precipitation/high elevation regions, and the South Fork is in a low precipitation/low elevation hydroregion (see *Appendix*). Finally, the North Fork lithology is distinct from that in the South Fork.

Data needs and remaining uncertainties: There is some historical information about the distribution of chinook in the Nooksack River Basin (Norgore and Anderson 1921), but the timing of adults returning to the river to spawn and their spawning distributions are not well known. In particular, it is unclear to which populations the early-returning chinook spawning in the Middle Fork of the Nooksack and the late-returning chinook throughout the Nooskack Basin belong. The co-managers consider the early-returning chinook in the Middle Fork to be part of the North Fork Nooksack stock (WDF et al. 1993), but there is insufficient evidence to date to evaluate whether fish in those two rivers were demographically connected historically, or whether historically accessible habitat in the Middle Fork Nooksack was of sufficient area to support an independent population. The origin of late-spawning chinook in the Nooksack River Basin also is not clear. There has been a long history of non-native hatchery releases in the Basin; and genetic analyses of late-spawning fish should help address whether those adults are offspring from hatchery releases or strays from other systems.

The extent to which present patterns of genetic distinctness between fish in the two forks represents historical patterns of distinctness is not known. The South Fork Nooksack stopped producing hatchery-origin chinook in 1993 (Marshall et al. 1995); yet inconclusive evidence suggests there may be introgression between late-spawning chinook and South Fork early spawners (Shacklee and Young 2000). The origin of the fish in the North Fork is not clear because of extensive hatchery inputs from the North Fork itself and releases of hatchery-origin fingerlings throughout the upper North Fork (WDF et al. 1993, Marshall et al. 1995, A. Marshall, pers. commun.) In addition, recent sampling of outmigrants from the Nooksack River Basin indicate that naturally produced smolts are in very low abundance relative to hatchery produced fish (Conrad and

MacKay 2000). In addition, the distribution of juvenile rearing areas for chinook born in the Nooksack River Basin is poorly understood. The small *t* value could suggest that differences between the two groups of fish are due to genetic drift arising in populations of small effective size. Therefore, the genetic distinctness between the North and South Fork Nooksack groups may not reflect historical patterns of reproductive isolation between the groups. The number of reported strays between forks of the Nooksack is fairly large, but until (1) the proportion of fish in each group that strays and (2) the proportion of spawners in each group made up of strays can be estimated, it is difficult to discern whether the fish moving between the forks are expected to influence one another's population or extinction dynamics. Length-at-age of fish from the two streams is not significantly different. This similarity may be due to recent exchanges due to hatchery transfers or due to phenotypically plastic responses to similar ocean or nearshore environments.

Skagit River Basin

Chinook in the Skagit River Basin occupy a large, diverse river drainage whose spawning reaches are geographically relatively far away from neighboring river basins (Fig. 1, Table 2). Genetically, the chinook in the Skagit River Basin are distinctive from chinook in other rivers in Puget Sound. Marshall et al. (1995) assigned all of the Skagit chinook salmon stocks and the Stillaguamish stocks to the same Genetic Diversity Unit (GDU), based on a number of life history, genetic, and habitat similarities within the Skagit and Stillaguamish River basins.

3. **lower Skagit River**
4. **upper Skagit River**
5. **lower Sauk River**
6. **Suiattle River**
7. **upper Sauk River**
8. **Cascade River**

Summary of information used in population structure decisions. Almost all of the chinook populations currently have disjunct spawning distributions, except for the chinook in the mainstem Skagit and lower Sauk rivers, whose spawning areas adjoin or are in close proximity (Fig. 1, Table 2). For example, the early-run spawning areas currently are separated from the late-run stocks lower in their tributaries by 8-10 miles of unsuitable spawning habitat (Marshall et al. 1995; Table 2). The genetic data suggest that there are 6 independent populations of chinook spawning in the Skagit River, although our confidence in this determination generally is not high (genetic independence scores for all pairs of sites are mostly 2's and a few 3's; Table 6). Support is strongest for identifying chinook in the Suiattle and Cascade Rivers as independent populations. Genetic similarities among groups of fish in the Skagit River Basin are relatively high—even when comparing late- and early-run stocks (Fig. 3). Nevertheless, G-tests for heterogeneity in allele frequencies between groups all are highly significant. WDF et al. (1993) report that all of the chinook stocks in the Skagit River Basin are of native origin and have not significantly interbred.

Summary of additional information. The only direct estimates of migration among chinook groups in the Skagit River Basin are strays recovered from other river

systems (e.g., strays from the North Fork of the Stillaguamish River have been recovered in the upper and lower Skagit River; see *Appendix*.) In addition, out-of-system strays collected at Baker trap in the lower Skagit River represent a high proportion of the trap return, and they come from as far away as Vancouver Island (B. Hayman, Skagit System Cooperative, pers. commun.) Similarly, hatchery-origin early and late-run chinook have been recovered in the Stillaguamish and Snohomish River basins. Coded-wire tag data reported by PSMFC indicate that in-basin chinook stocks reared at Marblemount Hatchery have been recovered in the mainstem Skagit as well as tributaries such as Illabot Creek, Jordan Creek, and the Cascade River. As for most of the CWT data, quantitative estimates of stray rates among stocks in the Skagit River Basin are not available. Length-at-age data from the upper and lower Skagit and lower Sauk chinook show those groups of fish clustering very closely together. In contrast, length at age for the 3 early-run groups in the Skagit is very different (see *Appendix*). Age distributions of early-run chinook in the Skagit Basin are somewhat distinct, but the Suiattle and upper Sauk groups cluster together in the UPGMA. In contrast, age distributions are distinct among the late-returning stocks in the Skagit Basin. As mentioned in the *Results*, groups of fish clustered based on similarity in age distributions do not match well with geographic proximity of clusters (unlike the length-at-age data). The spawn timing of the Suiattle chinook is distinctly earlier than that of the other two early-run stocks, and scale data suggest that Suiattle chinook also have a relatively high proportion of yearling outmigrants (Marshall et al. 1995).

Regardless of the model used to estimate correlations in abundance, the three late-run stocks in the Skagit Basin are always clustered together (see *Appendix*). In contrast, the two early-run stocks for which we have data consistently are very different in their abundances over time from all other Skagit Basin stocks. In general, the influence of hatchery stray chinook on current population dynamics of early-run chinook is thought to be low.

Chinook spawning in the lower Skagit and lower Sauk occur in the low precipitation/low elevation hydroregion, and the upper Skagit chinook occur in the low precipitation and low and high elevation hydroregions (see *Appendix*). All three early-run streams in the Skagit Basin have snowmelt-dominated hydrographs. The upper Cascade River is in the low precipitation/high elevation hydroregion, and the upper Sauk and Suiattle Rivers are in the high precipitation/high elevation hydroregion. The geology of the three river basins is somewhat distinctive. The lower Sauk and lower Skagit have similar lithologies, and the rock types in the upper Skagit are somewhat distinctive.

Remaining uncertainties and data needs: There is no information on the extent of straying that occurs among the 3 late-returning stocks within the Skagit River Basin. The contiguous spawning distribution of the chinook spawning in the lower Skagit, upper Skagit and lower Sauk suggests that it is possible that they are linked demographically. It is not known whether interpreting genetic data is complicated by past hatchery practices with late-run chinook (Green River stock origin) at the Skagit Hatchery. The genetic and life history data for the lower Sauk River fish are based on one sample year—1986. The extent to which this is representative of the chinook in the Sauk is not known. Broodstock collections for the Skagit Hatchery early-run chinook relied upon timing differences to separate spring, summer and fall chinook broodstocks, which was difficult because of overlap in the run timing distributions (Marshall et al. 1995). Genetic similarities among chinook stocks in the Skagit Basin may reflect some influence from hatchery strays and broodstock collection methods, so it is difficult to know whether

current patterns of genetic structure reflect what would have occurred before the hatchery. More extensive genetic sampling of stocks throughout the Skagit River Basin may help to clear up some of the uncertainties in population structure determinations, especially if sampling evenly spans the spatial extent of existing spawning areas.

Stillaguamish River Basin

Chinook in the Stillaguamish River Basin are geographically distinct from chinook in other major Puget Sound Basins. Their genetic composition does not neatly correspond to geographic proximity—the South Fork Stillaguamish chinook are most closely allied with chinook in the Snohomish River Basin, and the North Fork chinook cluster with Skagit Basin fish (Fig. 3). There have been a number of chinook from the North Fork of the Nooksack River (Kendall Creek hatchery) recovered in the North Fork Stillaguamish River. North Fork Stillaguamish chinook also have strayed into the upper and lower Skagit River and into the Snohomish River Basin (see *Appendix*). In addition to the genetic similarities, the age distribution and length-at-age of North Fork Stillaguamish chinook are more similar to chinook spawning in the lower portions of the Skagit River Basin than they are to chinook in the South Fork of the Stillaguamish. Nevertheless, the geographic distances separating Stillaguamish chinook spawning areas from other rivers and their population dynamics suggest that chinook in the Stillaguamish River Basin are not part of a larger population encompassing fish in other river basins.

9. North Fork Stillaguamish River
10. South Fork Stillaguamish River

Summary of information used in population structure decisions. There is strong genetic support for separating chinook in the Stillaguamish River Basin into two independent populations (independence score = 3; Table 6). The large θ value, estimate of *t* and genetic distances all suggest that the two populations have been genetically isolated for a long period of time. Genetically, the North Fork Stillaguamish chinook cluster with Skagit River Basin stocks—indeed, Marshall et al. (1995) included chinook from those two streams in the same GDU. In contrast, the South Fork Stillaguamish chinook cluster with Snohomish River Basin stocks (Fig. 3). The genetic similarity of North Fork Stillaguamish and Skagit chinook is consistent with historical patterns of river flow on geological time scales—10,000 years ago, the Sauk-Suiattle river systems flowed into the Stillaguamish watershed (Marshall et al. 1995). The origin of the North Fork Stillaguamish chinook is considered to be native; yet the origin of South Fork chinook is unknown (WDF et al. 1993).

Summary of additional information. Coded-wire tag data reported by PSMFC indicate that chinook reared at the Stillaguamish Tribal Hatchery on the North Fork have been recovered at North Fork tributaries such as the Boulder River and Squire Creek, but none have been recovered in the South Fork. The age distribution and length at age of chinook in the 2 forks of the Stillaguamish are distinct. As stated above, those life history characteristics of North Fork Stillaguamish are more similar to those of the late-run chinook in the Skagit River Basin than they are to the age distribution and lengths of the South Fork Stillaguamish chinook.

The population dynamics of the chinook in the 2 forks of the Stillaguamish River are relatively strongly correlated. The correlations in abundance over time are more

closely correlated between the North and South Forks of the Stillaguamish River than they are to any other groups of chinook in Puget Sound (see *Appendix*).

The habitat characteristics experienced by chinook in the 2 forks of the Stillaguamish are fairly similar. The hydrographs are both mixed: in the upper reaches of the streams they are a mixed snowmelt and rainfall hydrograph, and in the lower rivers, the hydrograph is rainfall dominated. Both streams are in the low precipitation/low elevation hydroregion, although the North Fork drains more high precipitation areas (see *Appendix*). Temperatures in the two streams are very similar. In contrast to the hydrology and temperature, the geological characteristics of the two forks are distinct, and each fork is in a different EPA ecoregion.

Remaining uncertainties and data needs: The genetic influences of releases of non-native fall chinook in the South Fork of the Stillaguamish, particularly Green River stock with similar spawn timing, is unknown (WDF et al. 1993). The cause for the genetic and life history similarities between North Fork Stillaguamish chinook and Skagit River late-run chinook is not well understood. In addition, the population status of the chinook spawning in the mainstem of the Stillaguamish River below the forks is not known.

Snohomish River Basin

Chinook in the Snohomish River Basin are geographically distinct from chinook in other Puget Sound streams (Fig. 1 and Table 2). Genetically, the Snohomish River chinook form a coherent cluster that includes the South Fork Stillaguamish and lower Skagit chinook (Fig. 3). Because of their genetic distinctness and the geographic distances separating the nearest spawning areas outside of the Snohomish River Basin, it is unlikely that chinook in the Snohomish River Basin are part of a larger population that includes chinook in rivers outside of the Snohomish.

11. Skykomish River
12. Snoqualmie River

Summary of information used in population structure decisions. Disjunct geographic locations of spawning grounds for chinook in the Snoqualmie and Skykomish River Basins support their delineation as separate populations. Chinook spawning in the mainstem Snohomish River are continuous in their distribution with those in the Skykomish; suggesting that unless genetic or other information becomes available, the Snohomish mainstem fish belong in the Skykomish River population. Genetic data indicate that chinook spawning in the Skykomish River Basin should be considered to be a separate population from those spawning in the Snoqualmie River Basin (genetic independence score = 2; Table 6). The Wallace and Bridal Veil stocks are genetically very similar to each other and to the Skykomish (genetic independence < 0), so those fish are included together within the Skykomish population. The Wallace River stock is heavily hatchery influenced, and its broodstock history includes a Green River stock, a Skykomish River summer stock, and possibly some wild stocks that have strayed (WDF et al. 1993). The sample of chinook from the Sultan River is genetically distinctive from the cluster containing fish from the Skykomish and Wallace rivers and Bridal Veil Creek, and it is also different from the Snoqualmie sample (genetic independence from stocks within the Snohomish Basin = 2; Table 6, Fig. 3.) The genetic distances separating the

Skykomish and Snoqualmie stocks in the Snohomish drainage are similar in magnitude to those separating populations in the Skagit River Basin. The Snohomish and Bridal Veil stocks are considered to be of native origin (WDF et al. 1993).

Summary of additional information. There is good documentation of straying of chinook from the Wallace hatchery throughout the Snohomish River Basin. Studies where the otoliths of hatchery fish were thermally mass-marked suggest that many of the naturally spawning chinook in the Skykomish River and its tributaries are strays from the Wallace Hatchery (K. Rawson, Tulalip Tribes, unpubl. data). In addition, strays from the Tulalip Hatchery make up a fraction of the naturally spawning chinook in the Snoqualmie system, especially in Tokul Creek. Wallace River hatchery fish are also occasionally found in the Snoqualmie system, but at very low levels.

Chinook from Bridal Veil Creek, Sultan, Wallace and Snohomish rivers cluster together based on age distributions. In contrast, the Snoqualmie chinook sample is very different in its age structure, possibly because it is only a single sample year. Length-at-age data suggest that Bridal Veil and Snoqualmie chinook are very similar (see *Appendix*). Wallace, Skykomish, and Sultan chinook are in a separate cluster based on the similarity in length at age of those fish. The distinct length at age of the Bridal Veil and Snoqualmie chinook may be due in part to the small number of years (2 and 1 years, respectively) included in those samples. There is very little overlap in spawn timing among any of the Snohomish River Basin stocks (Fig. 7).

The Pilchuck, Sultan, Snoqualmie and lower Skykomish chinook spawn in streams with a rainfall- dominated hydrograph. In contrast, Bridal Veil chinook experience a mixed hydrograph that exhibits snowmelt and rainfall peak flows. As a result of the hydrograph patterns, the Bridal Veil chinook spawn in the rainfall/snowmelt transition hydroregion, and all other chinook in the Snohomish River Basin are in the low precipitation/low elevation hydroregion (see *Appendix*.) Similar to their distinctive hydrograph characteristics, chinook in Bridal Veil creek spawn in habitats with different lithology and they are in a different EPA ecoregion than the other chinook in the Snohomish Basin.

Remaining uncertainties and data needs: Based on analyses to date, it is not clear in which population the chinook in the Snohomish River belong, including the chinook spawning in the Pilchuck River. Watershed area of the Pilchuck River is smaller than that of the smallest one for which we have identified an independent population—the South Fork Nooksack River (Fig. 2), so it is difficult to tell whether it is big enough to have supported an independent population. The population status of the Sultan River chinook is similarly uncertain, and its watershed area is also relatively small (Fig. 2). There are no straying data to indicate the levels of migration among Snohomish River Basin tributaries other than from hatchery chinook originating in the Wallace River. The unclear relationship of the chinook spawning in the lower Snohomish River and tributaries to the other chinook in the Snohomish River Basin makes their population status uncertain. The best way to classify these fish would be to conduct genetic sampling and analysis from the Pilchuck River and lower Snohomish, with concurrent sampling from the Skykomish and Snoqualmie populations. Samples from the South Fork Stillaguamish should also be collected at the same time because of the apparent relationship between this population and populations of chinook in the Snohomish system.

Lake Washington drainage

The unique physical orientation of streams draining into Lake Washington and a distinct, single outlet stream make it unlikely that chinook spawning in the Lake Washington drainage are part of a larger population of chinook that includes other river basins (Fig. 1). Interestingly, the population dynamics of chinook in Lake Washington (north Lake Washington tributaries and the Cedar River) and Duwamish/Green rivers are closely correlated (see *Appendix*.) It is likely that those correlations reflect similar patterns of hatchery releases, harvest levels or other environmental conditions rather than high rates of straying. The available stray data indicate that chinook do move between the Lake Washington (Issaquah hatchery) and Green/Duwamish river basins, but the number of recoveries is not high (see *Appendix*.) In addition, a few strays from south Puget Sound and the northern Kitsap peninsula have been recovered in Lake Washington and Issaquah Creek.

Genetic and life history data are not generally informative for reconstructing historical population structure relationships between chinook in the Lake Washington and other river basins in Puget Sound. The genetic composition of chinook in north Lake Washington is extensively influenced by hatchery stocks, mostly from the Green River broodstock. In contrast, the Cedar River Basin has not received many hatchery plants (WDF et al. 1993, Myers et al. 1998).

Prior to the Osceola Mudflow, the Cedar- Lake Washington basin and Green River drained independently to Puget Sound (Crandell 1963, Dragovich et al. 1994, Barnhardt et al. 1998). Nevertheless, for the purpose of identifying populations, the existing hydrologic connections were considered to be permanent over the next 100 years. Therefore, information on the historical connections between the Cedar, Lake Washington and Green/Duwamish river drainages was used to help interpret genetic and life history data, but we did not consider reconstruction or complete recovery of historical population structures.

13. Cedar River
14. north Lake Washington

Summary of information used in population structure decisions. Chinook spawning in north Lake Washington tributaries (including Issaquah Creek and Sammamish River drainages) and the Cedar River are considered to be separate populations (genetic independence score = 2; Table 6). Whether the collection of tributaries draining into north Lake Washington historically supported an independent population is not clear.

Summary of additional information. It is not known what (if any) contribution lake-spawning chinook in the lake Washington drainage may have made to an historical population of chinook in this region. The only straying data that are available for estimating movement of chinook throughout the Lake Washington drainage are for chinook from the Issaquah hatchery, and there are no reported recoveries of Issaquah chinook in other streams within the Lake Washington basin (see *Appendix*). The geographic separation between spawning areas in north Lake Washington and the Cedar River support the genetic separation of the two populations.

Potential environmental influences on observed correlations in abundance between Cedar River and north Lake Washington tributaries cannot be ruled out (e.g., correlations in harvest, hatchery releases, or other environmental characteristics that might occur between these drainages). Since there are no straying data to support the correlated population dynamics within Lake Washington, the abundance correlations are not useful as independent evidence for population structure. The cumulative catchment area of tributaries draining into north Lake Washington (including the Sammamish River, Swamp, North, Bear, Little Bear and Issaquah creeks) is over 60,000 ha, which is larger than the smallest watershed containing an independent population in our analyses (i.e., the South Fork Nooksack River) (Fig. 2).

Remaining uncertainties and data needs: The inability to reconstruct historical patterns of genetic similarity because of extensive Green River hatchery stock transfers is problematic. Are there areas in the Lake Washington drainage where Green River stock is no longer replenished in local broodstocks, and hatcheries have been taking fish only from local streams? If so, how long have introductions from Green River stock been stopped? This information will help determine whether slight genetic (e.g., Sammamish River) or life history distinctness may be indicative of a divergence due to selective differences (or drift)—and/or low dispersal. As stated above, information is needed clarifying whether the north Lake Washington tributaries historically supported a self-sustaining population of chinook, either before or after the extensive alterations to the lake level and outlet.

South Puget Sound

Genetic and life history data are not generally informative for reconstructing historical population structure relationships among chinook in the south Puget Sound and other river basins in Puget Sound. The genetic composition of existing chinook is extensively influenced by hatchery stocks, mostly from the Green River broodstock (WDF et al. 1993, Myers et al. 1998). Futhermore, the postglacial geomorphology of the lower Puyallup, White, and Duwamish River drainages in King and Pierce Counties has been radically transformed by episodic volcanic disturbances from Mount Rainier, the most recent of which was 600 years ago (Scott et al. 1995). As stated earlier, the population structure we describe below reflects the population structure of chinook populations 100 years ago, with the exception that more recent human-caused changes in flow to the White River are assumed to be permanent.

15. Green/Duwamish River

Summary of information used in population structure decisions. The Green/Duwamish River chinook are considered to be an independent population because of their relative geographic isolation from neighboring streams (Table 2). The historical connection between Lake Washington and the Green/Duwamish River (via the Black River) may have resulted in similar genetic composition of stocks in the two drainages, especially between the Cedar River and Green/Duwamish chinook. Similarly, the historical connection between the White River and the Green/Duwamish River may have resulted in genetically related chinook in those two river basins.

Summary of additional information. A few strays from Grovers Creek on the northern Kitsap peninsula have been recovered in the Green River, but the likely rate of straying is probably not enough to affect population dynamics of chinook in the two areas.

16. Puyallup River
17. White River

Summary of information used in population structure decisions. The Puyallup River Basin is probably sufficiently geographically isolated that chinook in the Puyallup are not part of a larger independent population encompassing other river basins (Fig. 1, Table 2). The closest river drainages—the Green/Duwamish and the Nisqually, are 83 and 60 km away, respectively. There are reported strays between the Puyallup and Green River basins, but the number of recoveries is very low (see *Appendix*). There are no reported strays between the Puyallup and Nisqually river basins. Population dynamics of chinook in the Puyallup, Nisqually and Green/Duwamish are completely uncorrelated (see *Appendix*).

As mentioned earlier, genetic and life history data for summer and fall chinook in south Puget Sound streams are not very informative for reconstructing historical population structure because of the extensive influence of Green River hatchery fish. Nevertheless, the genetic independence score for Puyallup and White River Chinook is a 3 (Table 6), indicating isolation between the two groups is enough to consider them as separate populations. The stock origin of Puyallup River late-run chinook is unknown due to the lack of coded wire tag and genetic information to determine hatchery influence on the naturally spawning population (WDF et al. 1993). The White River early-run hatchery and "wild" genetic samples are very similar to one another, reflecting the effects of the captive broodstock program begun in the 1970s (WDFW et al. 1996).

Summary of additional information. Historically, the White River early-run chinook population spawned in a greater proportion of the White River Basin—these areas above the Buckley trap are now not accessible to anadromous fish. The restricted spawning areas for the White River and Puyallup River chinook (above Electron Dam) may have resulted in more recent overlap in some use of habitat in relation to historical patterns of distribution in the White/Puyallup basin (WDFW et al. 1996, Puyallup Tribe HGMP 2000).

Coded-wire tagged chinook reared at the White River Hatchery have been recovered in tributaries of the Puyallup such as Voight Creek and South Prairie Creek, but the rate of straying from the White to the Puyallup appears to be low (see *Appendix*).

The age distributions of White River chinook (hatchery and wild) are similar to those of the Puyallup hatchery chinook. South Prairie Creek chinook are somewhat different in their age distribution from the White and Puyallup hatchery stocks, but they all occur in the same larger cluster based on general similarity. Length-at-age of White River chinook is very distinct from Puyallup River and South Prairie Creek chinook, which are similar to one another (see *Appendix*). Although the run-timings are distinct, the mean spawning date of South Prairie Creek chinook and White River early-run chinook are close to one another (Fig. 7).

Abundances of spawning early-run chinook in the White River are not correlated with other stocks, supporting the idea that White River chinook are a separate, independent population. The influence of the captive broodstock program on the

abundance of the White River chinook means that their population dynamics should not necessarily be considered to be those one would observe under natural conditions. Similarly, the Puyallup late-run chinook are not correlated in abundance with chinook in nearby streams, except for the Deschutes River chinook, which are not currently spawning under natural conditions (see *Appendix*). As stated above, the abundance of Puyallup River chinook may be influenced by the presence of hatchery fish.

The White River early-run chinook spawn in habitats that are distinctive from those in which the Puyallup River late-run chinook spawn. The hydrograph experienced by the early-run chinook in the White River is a mixed snowmelt and rainfall dominated one, and the Puyallup hydrograph is mostly rainfall dominated. As a result, the White River chinook spawn primarily in the snowmelt transition hydroregion, and the Puyallup fall chinook occur in the rainfall dominated hydroregion at lower elevations (see *Appendix*). Based on their historical distribution above Buckley trap, an even greater proportion of the White River chinook spawning areas would have been in the snowmelt transition hydroregion in the past. Temperatures in the Puyallup River are variable and not similar to the temperature in the White River. The chinook spawning areas in the White River have distinct lithology from the areas in which the Puyallup fall chinook spawn. Similarly, the two rivers occur in different EPA ecoregions.

Remaining uncertainties and data needs: The inability to reconstruct historical patterns of genetic similarity among chinook because of extensive Green River hatchery stock transfers is problematic. Whether the Puyallup River chinook should be considered to be part of a larger south Puget Sound population is not clear without better straying data and historical information on the distribution of spawning or rearing chinook in smaller tributaries throughout southern Puget Sound (e.g., Garrison Creek).

18. Nisqually River

Summary of information used in population structure decisions. The geographic location of the spawning grounds within the Nisqually River Basin suggests that historically, chinook in the Nisqually may have been an independent population from the chinook spawning throughout the rest of southern Puget Sound (Fig. 1, Table 2). Nisqually chinook show very minor genetic distinctions from other South Puget Sound chinook stocks. The stock origin for Nisqually chinook is believed to be a mixture of original stock and other south Puget Sound stocks (WDF et al. 1993).

Similar to the genetic data, life history data are not considered to be informative for reconstructing historical population structure in the Nisqually and south Puget Sound regions because of the presence of non-native chinook. In addition, the spawn timing of Nisqually and most other southern Puget Sound stocks is very similar (early October).

Summary of additional information. There are 3 dams on the Nisqually River that limit the present chinook from their historical spawning distributions. The low correlation in spawner abundance between the Nisqually and nearby rivers supports the idea that demographic connections between chinook in the Nisqually and other streams is fairly low (see *Appendix*). Nevertheless, because of the extensive presence of hatchery fish in spawning escapements and potential correlations in harvest rates on southern Puget Sound stocks, it is difficult to attach much significance to patterns of correlations in population dynamics for these groups.

Chinook spawning in the Nisqually and all of the southern Puget Sound streams experience the same rainfall-dominated hydroregion (see *Appendix*) and similar lithology. Chambers Creek and the Nisqually and Deschutes rivers are in a different EPA ecoregion than the rest of southern Puget Sound tributaries.

Remaining uncertainties and data needs: It is not clear whether chinook spawning (regularly or occasionally) in smaller south Puget Sound tributaries are part of a population that includes the Nisqually. It would be useful to summarize historical records of spawning presence, timing, and abundance of chinook in other southern Puget Sound streams so that their population structure could be estimated.

It is not clear to what extent miscellaneous streams in southern and central Puget Sound represent potentially demographically linked groups of chinook. Historical estimates of chinook spawning or presence in southern Puget Sound streams are not known. The chinook spawning in these smaller South Puget Sound streams may have been "sink" populations that were never very large historically, and that only contained spawning adults in significant numbers during years when self-sustaining runs in the South Sound (e.g., Nisqually, Puyallup) had strong returns. It is difficult to test this idea with existing data. There are recoveries of coded-wire tagged chinook throughout southern Puget Sound that suggest that at least hatchery chinook move readily within this region. For example, Garrison Hatchery has received stray chinook from the Nooksack River, Issaquah Creek, Green River, and Grovers Creek from the northern Kitsap peninsula (see *Appendix*). McAllister Hatchery (west of the Nisqually River) has received stray chinook from the Nisqually River, and from Garrison and Grovers Creek hatcheries. Capitol Lake (into which the Deschutes River flows) received stray chinook from Issaquah Creek and Grovers Creek hatcheries and from the Skokomish and Elwha rivers. Finally, chinook from throughout central and southern Puget Sound have been recovered in other south Puget Sound streams (such as Burley Creek, Coulter Creek, Minter Creek and Hupp Springs). The extent to which the straying behavior of hatchery chinook reflects behavior of native, naturally spawning fish under historical conditions is not known.

Hood Canal

Hood Canal streams are geographically relatively isolated from other streams in the Puget Sound ESU (Fig. 1). The two closest river basins to the Dosewallips at the northern end of Hood Canal are the Snohomish and Dungeness Rivers, which are 97 and 103 km away, respectively (Table 2). Because of its geographic location, it is unlikely that chinook spawning in Hood Canal streams are part of a larger demographically independent population that includes streams outside of Hood Canal. There are not good straying data to support this assertion—nevertheless, the only coded wire tag recoveries reported in Hood Canal that come from out of the region were chinook from the Elwha hatchery recovered at Hoodsport, at the northern end of Hood Canal.

19. Skokomish River

Summary of information used in population structure decisions. Chinook returning to the Skokomish River in Hood Canal are an independent population. Genetic data are not expected to be informative in reconstructing population structure under

historical conditions, since many (if not all) of the chinook spawning in Hood Canal streams are thought to be of hatchery origin (A. Marshall, WDFW, pers. commun.). In support of this idea, Hood Canal chinook cluster genetically with South Puget Sound streams, all of which have been stocked with Green River broodstock (Fig. 3).

Similar to genetic data, life history information is not expected to be helpful in estimating population structure in Hood Canal. Mean spawn timing in all Hood Canal rivers (ranging from mid-September to early October) is somewhat earlier than in southern Puget Sound.

Summary of additional information. Spawner age at Hood Canal and George Adams hatcheries are highly dissimilar. Chinook spawning in streams in Hood Canal do not have to travel far to stray between streams. Furthermore, the spawning areas available are mostly in the lower reaches of the streams because of the high gradient regions of the eastern Olympic mountains in which they occur. The watershed areas of the Hamma Hamma, Dosewallips and Duckabush Rivers are smaller than that of the South Fork of the Nooksack River (Fig. 2), so it is difficult with existing information to determine whether they are large enough to have supported independent populations of chinook.

The only straying data available are recoveries of chinook from the Skokomish hatchery program. The Hoodsport Hatchery has received a number of chinook from the Skokomish River, possibly because of its strategic location at the mouth of Hood Canal.

Correlations in abundance of spawners suggests that the chinook in the Dosewallips, Duckabush, Hamma Hamma and Skokomish are relatively demographically isolated from one another. Nevertheless, these patterns of population dynamic correlations are suspect because the methods for estimating abundance in the northern Hood Canal streams are inconsistent over time (Comp chinook group, pers. commun.)

The Dosewallips River Basin is the only river in Hood Canal that occurs in the snowmelt-transition hydroregion (see *Appendix*). Likewise, the Skokomish River Basin is distinguished in its lithology from the other Hood Canal streams. Otherwise, habitat characteristics chinook experience in Hood Canal streams are similar.

Remaining uncertainties and data needs: The population status of chinook spawning in other Hood Canal streams is not clear. Chinook in these smaller streams may never have occurred in very high abundance. One possible scenario of population structure is that historically, the Skokomish River supported one or more self-sustaining populations of chinook, and that the Dosewallips, Duckabush and Hamma Hamma rivers had chinook spawners whose numbers were largely driven by the Skokomish "source" population. In other words, the smaller Hood Canal rivers might have supported "sink" populations that had relatively numerous spawners during years of especially high returns to the Skokomish. Alternatively, the Dosewallips, Duckabush and Hamma Hamma rivers historically could have supported small but self-sustaining populations of chinook. It is very difficult to distinguish between these alternative scenarios given the data that presently are available. Because genetic data are not representative of historical relationships among chinook in the different Hood Canal streams, the plausibility of the 3 northern Hood Canal rivers being able to support distinct, self-sustaining populations needs to be examined using other evidence. Documentation of the amount of chinook spawning and rearing habitat in Hood Canal streams under historical conditions will help in determining the likelihood that several independent populations of chinook existed historically in Hood Canal. Estimates of straying among Hood Canal streams are

lacking. In addition, the length of time certain broodstocks have been introduced into the Skokomish and Hoodsport hatcheries would be useful information to help interpret the potential biological significance of differences in life history data we have amassed thus far. Finally, independent and consistent sampling to estimate spawner escapements is needed for each of the 4 main western Hood Canal streams.

Strait of Juan de Fuca

20. Dungeness River

Summary of information used in population structure decisions. Genetically, chinook in the Dungeness River are distinctive from other fish in the Puget Sound—they are intermediate in their genetic composition between chinook in eastern Puget Sound and chinook in the Elwha River (A. Marshall, WDFW, pers. commun.). The chinook spawning in the Dungeness River are relatively physically isolated from chinook in nearby streams, supporting the conclusion that the Dungeness historically supported an independent population of chinook salmon.

Spawn timing data were the only life history data available for our analyses to date. Mainstem Dungeness chinook spawn around the same time as North Fork Stillaguamish and other "summer-run" chinook, but spawning in the Grey Wolf River is very early, similar to chinook spawning in the Suiattle River tributaries.

Summary of additional information. New information from the Dungeness captive broodstock program on straying of chinook from the Dungeness River is expected beginning in 2000 (B. Sele, pers. commun.). The abundance of chinook in the Dungeness has been extremely low for a number of years, and the captive broodstock program underway is designed to help restore the population. Correlations in abundance between chinook in the Dungeness River and others are consistently low—although it is difficult to attach much significance to those analyses because of the hatchery restoration efforts underway.

The Dungeness River has a fairly large spawning area accessible to chinook, and it reaches into the snowmelt transition hydroregion (see *Appendix*). The unique habitat characteristics of the Dungeness River (Marshall et al. 1995) supports the idea that the Dungeness probably historically supported an independent population of chinook salmon.

21. Elwha River

Summary of information used in population structure decisions. Genetic information suggests that the chinook salmon in the Elwha River were distinctive from the chinook further East along the Strait and in Puget Sound (Fig. 3). This population of chinook probably included those in the Elwha River Basin, which historically contained a population of the largest chinook salmon in the Puget Sound area, and smaller streams that drain directly into the Strait of Juan de Fuca (e.g., Morse Creek). It is thought that the historical run-timing of chinook in the Elwha River Basin was early May-October (Lichatowich 2000). The historical boundaries of the Elwha River population have been severely constrained because of the two dams on the river, so much of the evidence pertaining to the population structure relies on historical information about the amount of habitat available to spawning and rearing chinook salmon.

Summary of additional information. Coded-wire tag data suggest a fairly low rate of straying of chinook from the Elwha Hatchery to other streams in the Strait of Juan de Fuca and south Puget Sound (see *Appendix*).

Spawn timing of Elwha chinook is similar to "summer-run" stocks (and is earlier than southern Puget Sound stocks.) We do not have other life history data for comparison of Elwha chinook to other Puget Sound streams as of this writing.

The population dynamics of the Elwha River chinook are very distinctive from that of nearby streams (see *Appendix*). However, it is difficult to interpret these data because of the extensive influence of hatchery strays on the abundance of Elwha River chinook (WDF et al. 1993).

Historically, the Elwha chinook certainly would have experienced the snowmelt transition hydroregion (see *Appendix*). Similarly, the geology of the Elwha River Basin is distinctive from that of other streams nearby. In addition, the Elwha River is considered to be in different EPA ecoregions than other streams in Puget Sound.

Remaining uncertainties and data needs: What was relationship between Elwha chinook and chinook spawning in smaller streams along the Strait of Juan de Fuca?

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Table 1. Puget Sound chinook streams from which samples are used in this study and commonly used abbreviations.

River Basin Tributary	Abrreviations
Nooksack River Basin	
North Fork Nooksack River	nf.nook, Nooksack spring/summer
Kendall Creek	nf.nook, Nooksack spring/summer
Canyon Creek	nf.nook, Nooksack spring/summer
South Fork Nooksack River	sf.nook, Nooksack spring/summer
Miscellaneous north Puget Sound streams	Misc. 7A
Samish River	
Skagit River Basin	
Lower Skagit River	lw.skag, lower Skagit fall
Upper Skagit River	up.skag, upper Skagit summer
Lower Sauk River	lw.sauk, lower Sauk summer
Upper Cascade River	Upper Cascade spring
Ilabot Creek	Upper Cascade spring
Bacon Creek	Upper Cascade spring
Suiattle River	Suiattle spring
Big Creek	
Tenas Creek	
Buck Creek	
Lime Creek	
Sulphur Creek	
Upper Sauk River	Upper Sauk spring
Stillaguamish River Basin	
North Fork Stillaguamish River	nf.stilla or stilla.su, Stillaguamish summer
Squire Creek	nf.stilla or stilla.su, Stillaguamish summer
South Fork Stillaguamish River	sf.stilla or stilla.fa, Stillaguamish fall
Jim Creek	sf.stilla or stilla.fa, Stillaguamish fall
Snohomish River Basin	
Snohomish River	Snohomish summer, Snohomish fall
Pilchuck River	Snohomish fall
Skykomish River	Snohomish summer, snoho.su
Wallace River	Wallace summer/fall
Bridal Veil Creek	Bridalv, Bridal Veil Creek fall, Snohomish fall
Sultan River	Snohomish summer
Snoqualmie River	Snohomish fall
Tolt River	Snohomish fall
Lake Washington Basin	Lake Washington summer/fall
Sammamish	n.lkwash tribs
Swamp Creek	n.lkwash tribs

Table 1 (Continued).

River basin Tributaries	Abbreviations
North Creek	n.lkwash tribs
Big Bear Creek	n.lkwash tribs
Cottage Lake Creek	n.lkwash tribs
Issaquah	n.lkwash tribs
Holder Creek	n.lkwash tribs
Cedar River	Lake Washington summer/fall
Green River Basin	Green/Duwamish summer/fall
Crisp Creek	Green/Duwamish summer/fall
Clarks Creek	Green/Duwamish summer/fall
Duwamish	duwam.gr, Green/Duwamish summer/fall
Newaukum Creek	duwam.gr, Green/Duwamish summer/fall
Puyallup River Basin	Puyallup River fall
White River	White River spring
Stuck River	White River spring
Boise Creek	White River spring
Clearwater Creek	White River spring
Greenwater River	White River spring
Puyallup River	Puyal, Puyallup River fall
Carbon River	Puyal, Puyallup River fall
South Prairie Creek	Puyallup River fall
Nisqually River Basin	Nisqually River summer/fall, nisqua
Ohop Creek	Nisqually River summer/fall, nisqua
Kapowsin Creek	Nisqually River summer/fall, nisqua
Deschutes River	
Miscellaneous South Puget Sound streams	Misc.
Skookum Creek	Misc. 13B
Coulter Creek	Misc. 13A
Burley Creek	
Blackjack Creek	Misc. 10E
Gorst Creek	Misc. 10E
Clear Creek	Misc. 10E
Dogfish Creek	
Hood Canal	Hood Canal summer/fall
Skokomish River	Hood Canal summer/fall
Hamma Hamma River	Hood Canal summer/fall
Dosewallips River	Hood Canal summer/fall
Duckabush River	Hood Canal summer/fall
Strait of Juan de Fuca	
Dungeness River	
Grey wolf River	
Elwha River	

Table 2. Distances (km) separating the spawning grounds of Puget Sound chinook stocks. Spawning distributions are based on WDF et al. (1993). Distances were calculated as the shortest nautical distance separating each pair of sampling sites, including the river distance plus the distance between river mouths where applicable. Distances were measured using GIS software and a 1:250,000 scale map.

	sf.nook	samish	lw. Skag	up. Skag	lw. Sauk	up. Sauk	suiattle	stilla.su	stcilla.f	snoho.su	snoho.f	wallace	cedar	n. lkwash	duwam.gr	puyal	white	nisqua	deschu	misc.13a	misc.13b	skok	hamma	ducka	dosewal	dungen	elwha
sf.nook	0	94	154	210	224	262	257	241	221	216	214	258	231	226	217	263	265	260	292	289	285	240	217	202	199	142	168
samish	94	0	103	159	173	211	206	190	170	165	163	207	180	175	166	212	214	209	241	238	234	189	166	151	148	91	117
lw.skag	154	103	0	38	38	50	45	125	107	110	110	162	159	151	143	189	188	186	219	217	210	199	178	159	157	95	120
up.skag	210	159	38	0	0	37	32	194	176	179	179	232	228	222	212	258	259	258	288	289	282	268	247	231	229	164	189
lw.sauk	224	173	38	0	0	10	12	194	176	179	179	232	228	222	212	258	259	258	288	289	282	268	247	231	229	164	189
up.sauk	262	211	50	37	10	0	29	231	213	217	217	259	265	259	249	295	296	295	325	326	319	305	284	268	266	202	226
suiattle	257	206	45	32	12	29	0	226	208	212	212	254	260	254	244	290	291	290	320	321	314	300	279	263	261	197	221
stilla.su	241	190	125	194	194	231	226	0	0	77	77	130	128	123	112	161	163	159	187	190	183	167	145	131	130	136	167
stilla.f	221	170	107	176	176	213	208	0	0	58	58	100	110	105	97	145	145	141	172	172	165	152	130	113	112	121	152
snoho.su	216	165	110	179	179	217	212	77	58	0	0	0	95	90	80	128	128	126	158	157	150	139	117	98	97	103	134
snoho.f	214	163	110	179	179	217	212	77	58	0	0	9	104	99	88	137	137	134	166	165	158	147	125	106	105	112	142
wallace	258	207	162	232	232	259	254	130	100	0	9	0	148	141	133	181	179	177	211	208	201	192	170	149	148	156	187
cedar	231	180	159	228	228	265	260	128	110	95	104	148	0	71	60	107	113	111	137	140	135	163	139	129	126	129	162
n.lkwash	226	175	151	222	222	259	254	123	105	90	99	141	71	0	55	102	102	100	132	129	124	158	134	118	115	124	157
duwam.gr	217	166	143	212	212	249	244	112	97	80	88	133	60	55	0	83	83	70	108	101	95	151	125	109	106	118	148
puyal	263	212	189	258	258	295	290	161	145	128	137	181	107	102	83	0	0	60	93	90	83	199	175	158	155	166	199
white	265	214	188	259	259	296	291	163	145	128	137	179	113	102	83	0	0	60	93	90	83	199	175	158	155	166	199
nisqua	260	209	186	258	258	295	290	159	141	126	134	177	111	100	70	60	60	0	35	33	28	197	171	155	154	161	190
deschu	292	241	219	288	288	325	320	187	172	158	166	211	137	132	108	93	93	35	0	39	18	229	206	188	186	196	225
misc.13a	289	238	217	289	289	326	321	190	172	157	165	208	140	129	101	90	90	33	39	0	33	229	206	188	186	196	225
misc.13b	285	234	210	282	282	319	314	183	165	150	158	201	135	124	95	83	83	28	18	33	0	224	201	183	181	191	220
skok	240	189	199	268	268	305	300	167	152	139	147	192	163	158	151	199	199	197	229	229	224	0	25	24	37	147	177
hamma	217	166	178	247	247	284	279	145	130	117	125	170	139	134	125	175	175	171	206	206	201	25	0	14	21	121	154
ducka	202	151	159	231	231	268	263	131	113	98	106	149	129	118	109	158	158	155	188	188	183	24	14	0	8	106	134
dosewal	199	148	157	229	229	266	261	130	112	97	105	148	126	115	106	155	155	154	186	186	181	37	21	8	0	103	131
dungen	142	91	95	164	164	202	197	136	121	103	112	156	129	124	118	166	166	161	196	196	191	147	121	106	103	0	37
elwha	168	117	120	189	189	226	221	167	152	134	142	187	162	157	148	199	199	190	225	225	220	177	154	134	131	37	0

Table 3. Stocks of Puget Sound chinook, showing data years used in population genetic analyses reported in this document and the availability of data on genetic structure, age at reproduction, and spawner abundance (note that 'stock' is loosely defined here to mean any group of fish for which data were available. Stock names follow Myers et al. (1998) and WDF et al. (1993). 'H' in a stock name indicates that the stock is hatchery-produced. In the data columns, 'Y' indicates that data were available and 'ND' indicates that data were not available.

Stock name	Data years for genetics	Genetic data/age at reproduction	Abundance data
Misc streams, Area 7A		ND	Y
NF Nooksack R. Sp/Su H	1988, 1993	Y (H)	ND
SF Nooksack R. Sp/Su	1993-95, 1998	Y	Y
Samish R. Fa	1986	Y	Y
Lower Skagit R. Fa	1986-88, 1998	Y	Y
Upper Skagit R. Su	1986, 1994-95	Y	Y
Lower Sauk R. Su	1986	Y	Y
Upper Sauk R. Sp	1986, 94, 98	Y	Y
Suiattle R. Sp	1986-90, 1998	Y	Y
Upper Cascade R. Sp	1993-94	Y	ND
Stillaguamish R. Su	1987-88, 1996	Y	Y
Stillaguamish R. Fa	1992-96	Y	Y
Snohomish R. Su (Sky)	1988-89, 93, 1996	Y	Y
Snohomish R. Fa (Snoq.)	1988	Y	Y
Wallace R. Su/Fa	1988-89	Y	Y
Skykomish R. Su/Fa H	1987	Y (H)	ND
Bridal Veil Cr. (SF Sky) Su	1987-88	Y	ND
Misc streams, Area 10		ND	Y
Issaquah Cr. Su/F H	1992	Y (H)	ND
North Lk. Wash. tribs Su/Fa	1998	Y (Sammamish)	Y
Cedar R. Su/Fa	1993-94	Y	Y
Duwamish/Green R. Su/Fa	1987-88, 90, 1998	Y (H)	Y
Newaukum Cr. Su/Fa	1992-93	Y	ND
Puyallup R. Su/Fa	1992-93	Y (H)	Y
White R. Sp	1995-97	Y	Y
Nisqually Su/Fa	1998-99	Y	Y
Deschutes R. Su/Fa	1987	Y (H)	Y
Misc streams, Area 13		ND	Y
Misc streams, Area 13A		ND	Y
Misc streams, Area 13B		ND	Y
Misc streams, Area 10E		ND	Y
Skokomish R. Su/F	1998	Y	Y
Hamma Hamma R. Su/F		ND	Y
Duckabush R. Su/F		ND	Y
Dosewallips R. Su/F		ND	Y
Dungeness R. Su/F		ND	Y
Elwha R. Su/F	1988, 1991	Y(H)	Y

Table 4. Estimates of genetic differentiation among groups (θ) and gene flow separating groups (*Nm*) from 29 polymorphic allozyme loci in Puget Sound chinook salmon. The name of the groups being compared as the "total" for genetic variation and the number of groups included in each comparison are reported. Upper and lower 95% confidence intervals were determined by bootstrapping (see text).

Group name	n groups	θ	upper C.I.	lower C.I.	Nm
Puget Sound	33	0.063	0.113	0	3.72
Nooksack	2	0.019	0.036	0.003	13.12
Skagit	6	0.031	0.053	0.008	7.81
Skagit "springs"	3	0.023	0.043	0.004	10.62
Skagit "sum/fall"	3	0.009	0.016	0.004	27.53
Stillaguamish	2	0.027	0.048	0.010	9.01
Snohomish	5	0.009	0.019	0.001	27.53
Lake Wash.	3	0.014	0.024	0.006	17.61
south Sound	6	0.002	0.006	-0.002	124.75
Hood Canal	2	0.014	0.031	0.003	17.61

Table 5. Known spawning aggregations of chinook salmon in the Puget Sound ESU. Nomenclature follows that described in the SASSI document (WDF et al. 1993).

Geographic area	SASSI stock	Spawning aggregation
Nooksack/Samish	North Fork Nooksack	mainstem
		lower middle Fork Nooksack River
		Maple creek
		Canyon creek
		Cornell creek
		Boyd creek
		McDonald creek
	South Fork Nooksack	mainstem
	Samish/Mainstem Nooksack fall	mainstem Nooksack River
		Samish
Skagit	Upper Skagit mainstem/tribs summer	mainstem
		Ilabot creek
		Bacon creek
		Falls creek
		Goodell creek
		Clark creek
		Diobsud creek
	Lower Skagit mainstem/tribs fall	mainstem
	Lower Sauk summer	mainstem
	Upper Sauk spring	mainstem
		White Chuck River
		South Fork Sauk River
	Suiattle spring	Mainstem
		Sulphur creek
		Buck creek
		Big creek
		Lime creek
	Upper Cascade spring	mainstem
Stillaguamish	Stillaguamish summer	North Fork Stillaguamish River
		Boulder River
	Stillaguamish fall	South Fork Stillaguamish River
		mainstem Stillaguamish River
		Jim creek
		Canyon creek
Snohomish	Snohomish summer	mainstem Snohomish
		mainstem Skykomish
	Wallace summer/fall	mainstem
	Snohomish fall	Snoqualmie River
		Sultan River
		Pilchuck River
		Woods creek
		Elwell creek
		Tolt River
	Bridal Veil Creek fall	Bridal Veil creek
		South Fork Skykomish River
		North Fork Skykomish River
Lake Washington	Issaquah	Issaquah Creek
		East Fork Issaquah Creek

Table 5 (Continued).

Geographic area	SASSI stock	Spawning aggregation
	North Lake Washington tribs	North Creek
		Swamp Creek
		Bear Creek
		Little Bear Creek
		Thornton Creek
		McAleer Creek
		Cottage Lake Creek
		Sammamish River
	Cedar summer/fall	mainstem
Duwamish/Green	Duwamish/Green summer/fall	Duwamish River
		Green River
	Newaukum Creek	
Puyallup	White (Puyallup) spring	mainstem
		Clearwater River
		Greenwater River
		West Fork White River
	White (Puyallup) summer/fall	mainstem
		Clearwater River
		Greenwater River
	Puyallup fall	mainstem
		South Prairie Creek
		Carbon River
Nisqually	Nisqually summer/fall	Mainstem
		Ohop Creek
		Mashel River
South Sound	South sound tribs summer/fall	McAllister Creek
		Grovers Creek
		Gorst Creek
		Chambers Creek
		Carr Inlet streams
		Deschutes River
Hood Canal	Hood Canal	Skokomish River
		Hamma Hamma River
		Dosewallips River
		Duckabush River
		Union River
		Tahuya River
		Dewatto River
Strait of Juan de Fuca	Dungeness spring/summer	Mainstem
		Gray Wolf River
	Elwha/Morse Creek summer/fall	Elwha River
		Morse Creek

Table 6. Median independence scores (n = 10 scorers) based on genetic data for groups of chinook salmon in Puget Sound watersheds. See text for discussion of genetic data considered in these scores.

NOOKSACK	sf.nook	nf.nook
sf.nook	*	3
nf.nook		*

SKAGIT	lw.skag	up.skag	lw.sauk	up.sauk	suiattle	cascade
lw.skag	*	2	2	2	3	3
up.skag		*	2	2	2	2
lw.sauk			*	2	2	2.5
up.sauk				*	2	2
suiattle					*	2
cascade						*

STILLAGUAMISH	nf.stilla	sf.stilla
nf.stilla	*	3
sf.stilla		*

SNOHOMISH	lw.snoh	skykom	sultan	wallace	bridalveil	snoqual
lw.snoh	*	0	0	0	0	0
skykom		*	2	-2	-2	2
sultan			*	1	2	2
wallace				*	-3	1
bridalveil					*	1
snoqual						*

LK. WASHINGTON	cedar	nlk.wash	sammam	issaquah
cedar	*	0	2	2
nlk.wash		*	0	0
sammam			*	1
issaquah				*

SOUTH SOUND	duwam.gr	puyallup	white	nisqually	deschut
duwam.gr	*	1	3	1	0
puyallup		*	3	2	0
white			*	3	0
nisqually				*	0
deschut					*

HOOD CANAL	skokom	hamma	ducka	dosewal
skokom	*	-1	0	0
hamma		*	0	0
ducka			*	0
dosewal				*

Table 7. Proposed demographically independent populations of chinook salmon in the Puget Sound ESU.

Population
North Fork Nooksack River
South Fork Nooksack River
Lower Skagit River
Upper Skagit River
Lower Sauk River
Suiattle River
Upper Sauk River
Cascade River
North Fork Stillaguamish River
South Fork Stillaguamish River
Skykomish River
Snoqualmie River
North Lake Washington
Cedar River
Green/Duwamish River
Puyallup River
White River
Nisqually River
Skokomish River
Dungeness River
Elwha River

Figure 1. Distribution of chinook salmon SASSI stocks in Puget Sound (WDF et al. 1993). Colored, shaded areas indicate locations of primary spawning areas of chinook in Puget Sound streams. Colors refer to run timing types as identified in the SASSI document: Red: fall; Yellow: summer/fall; Green: summer; Orange: spring/summer; Blue: spring.

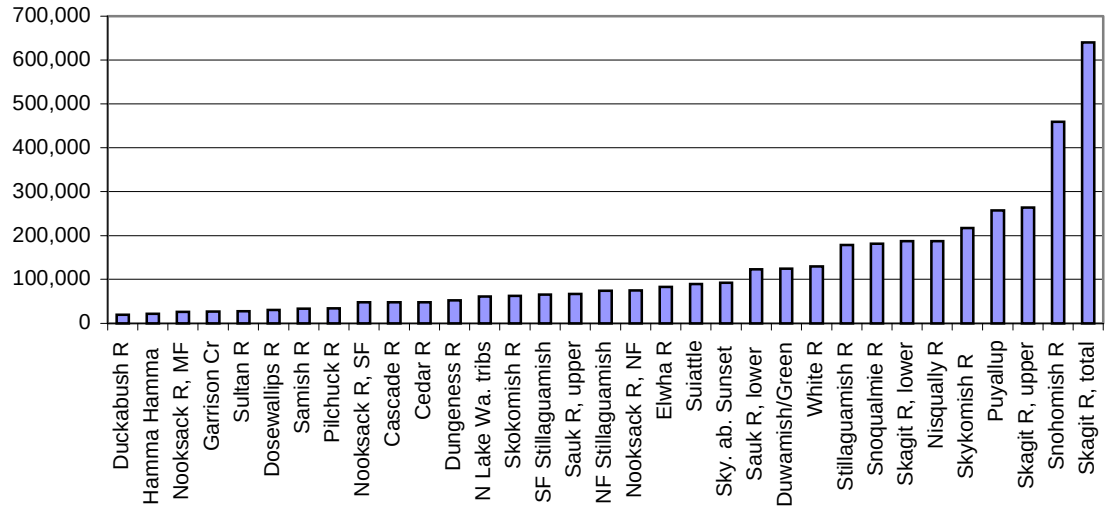

Figure 2. Basin area (ha) of rivers in Puget Sound.

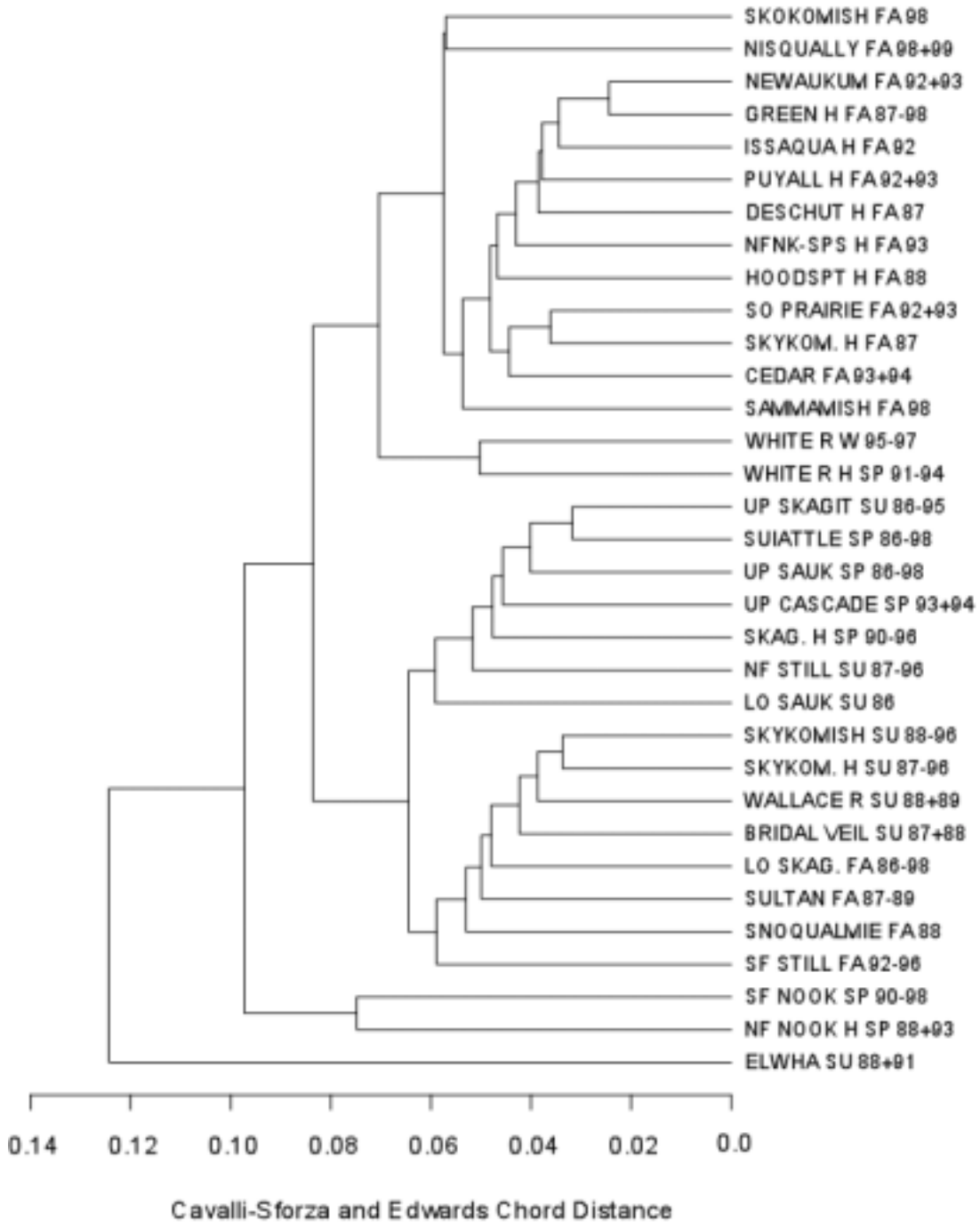

Figure 3A. UPGMA dendrogram of chinook salmon in Puget Sound streams. Similarity of chinook in the tree is based on genetic distances (Cavalli-Sforza Edwards chord distance) between groups of fish from different streams. Each sample includes at least 50 fish sampled as carcasses from spawning grounds in the named stream. Samples span multiple brood years (1980-1996), and brood years are pooled within sites for genetic distances calculated for this dendrogram. Years following stream name indicate range of sample years—see Table 3 for actual years sampled. Genetic analyses within sites detected among-brood year variation, but the genetic variation among sites was greater (A. Marshall and C. Busack, WDFW, unpubl. data).

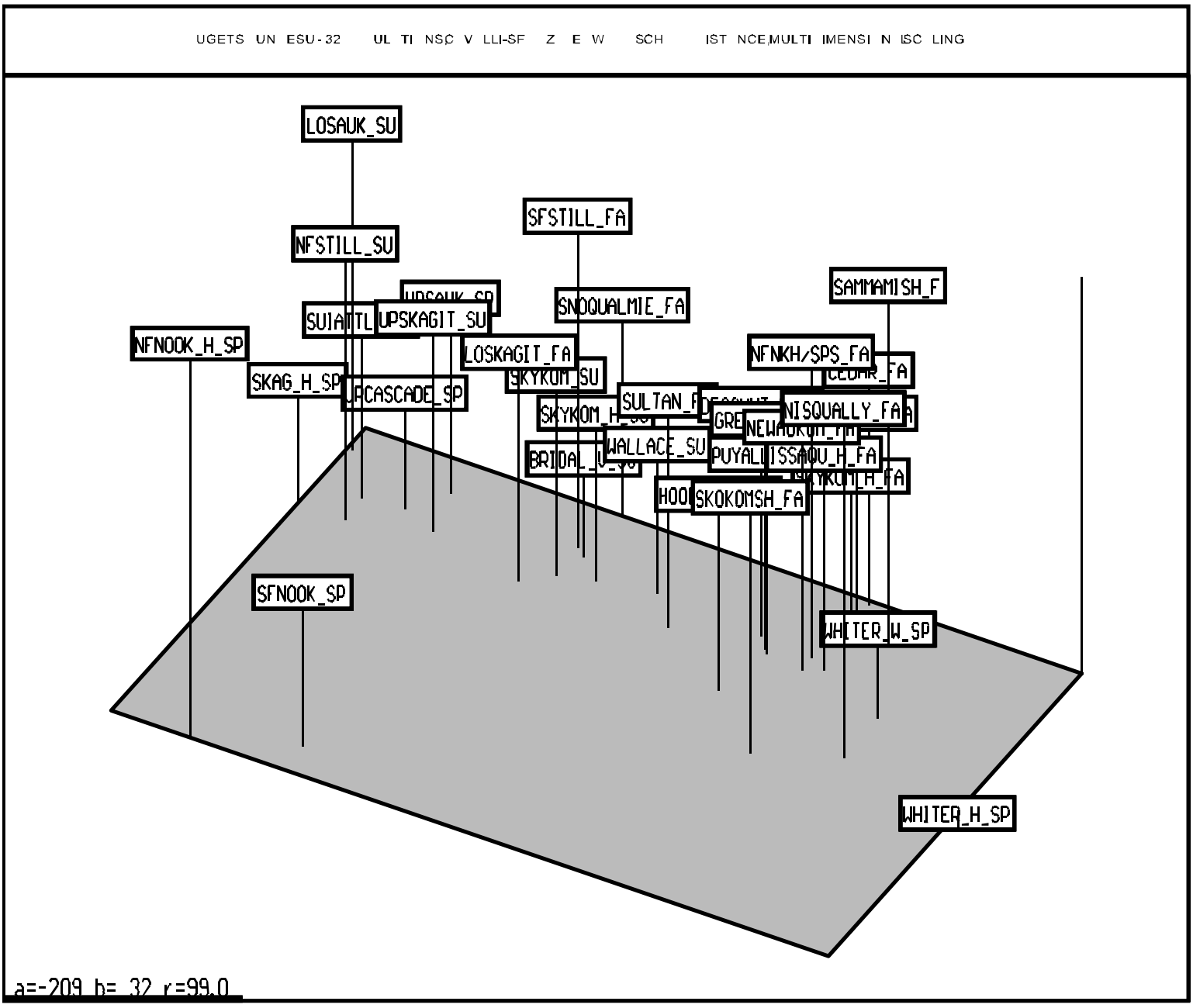

Figure 3B. Multi-dimensional scaling (MDS) plot using the same samples as are included in Fig. 3A.

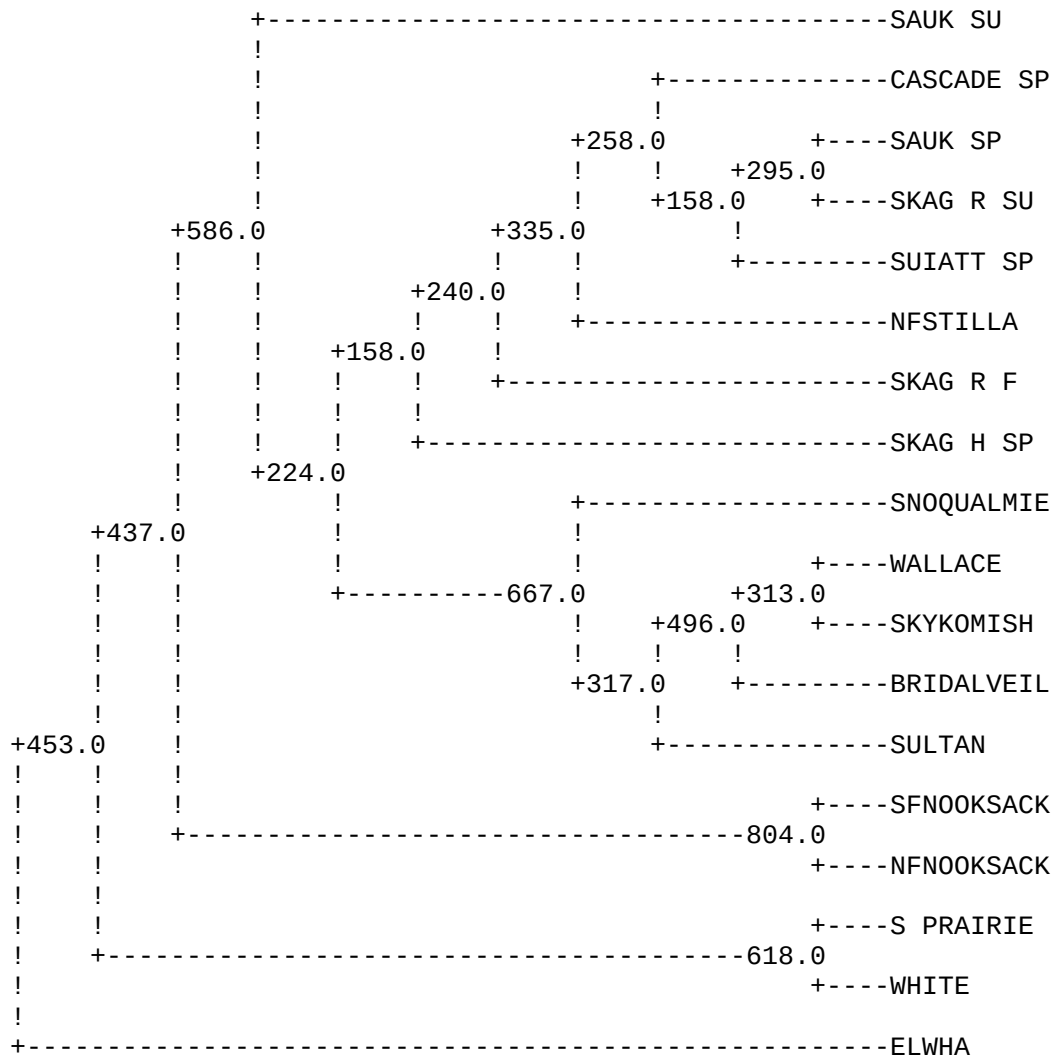

Figure 4. Bootstrapped genetic dendrogram for Cavalli-Sforza and Edwards (1967) chord distance based on allozyme frequencies. The allozyme dataset was bootstrapped over loci to generate 1000 resampled distance matrices and corresponding UPGMA dendrograms. In the consensus tree shown here, the number at each node indicates how many times the cluster to the right of that node occurred, out of 1000 bootstrapped topologies.

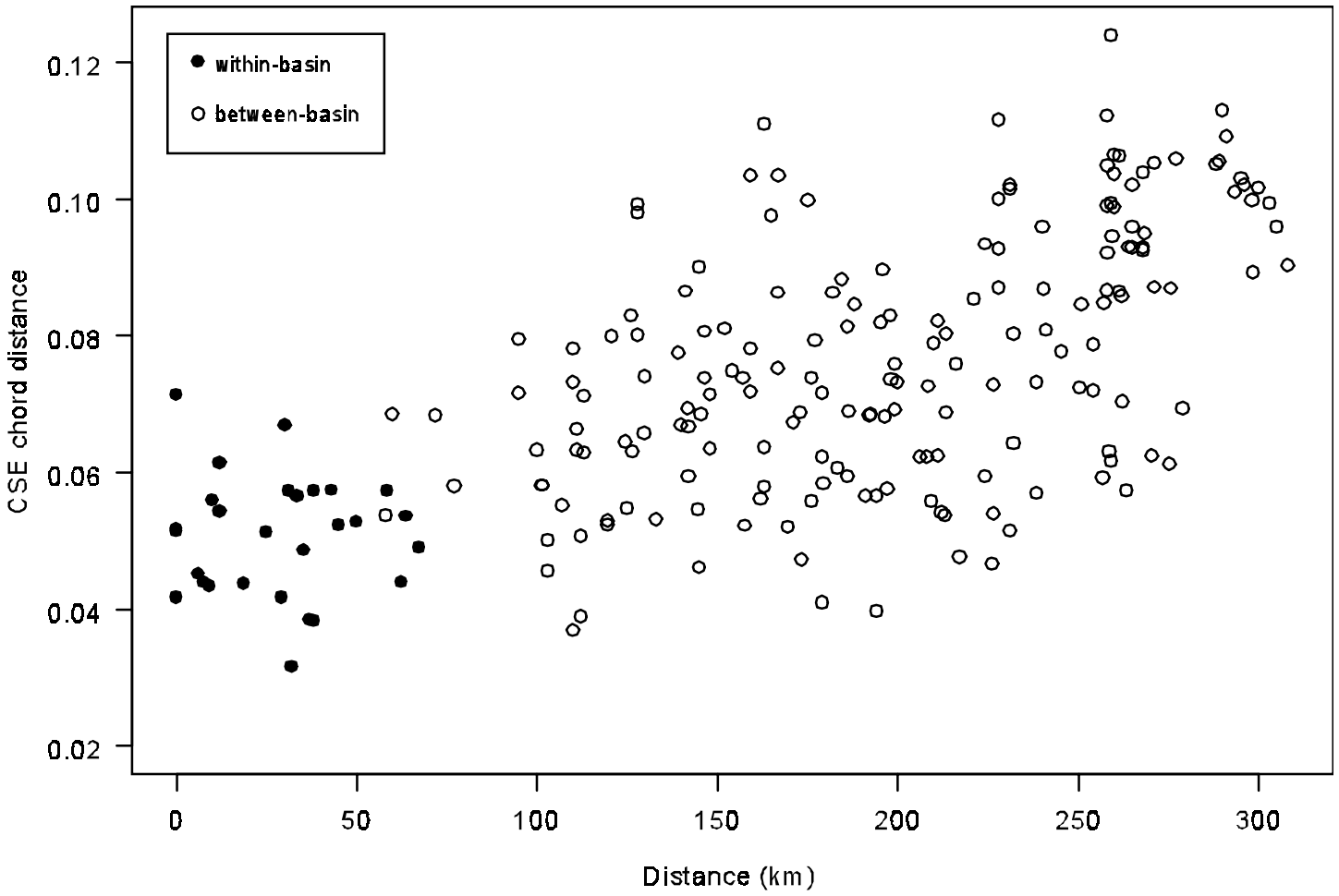

Figure 5. Relationship between geographic isolation and genetic dissimilarity of Puget Sound chinook stocks. The genetic distance between each pair of stocks is plotted against the geographic distance separating the spawning areas of those stocks. The analysis includes 15 naturally spawning stocks. Genetic distances (Cavalli-Sforza and Edwards 1967) are based on allozyme frequencies of carcasses sampled on the spawning grounds. The shortest nautical distance separating each pair of spawning reaches (river distance plus distance between river mouths) was measured using a 1:250,000 scale map and GIS software. A one-tailed Mantel test with 2000 bootstrap resamples detected a significant positive association between geographic and genetic distance ($P < 0.001$). Filled circles indicate comparisons between stocks within a major river basin; open circles indicate comparisons between stocks in different basins.

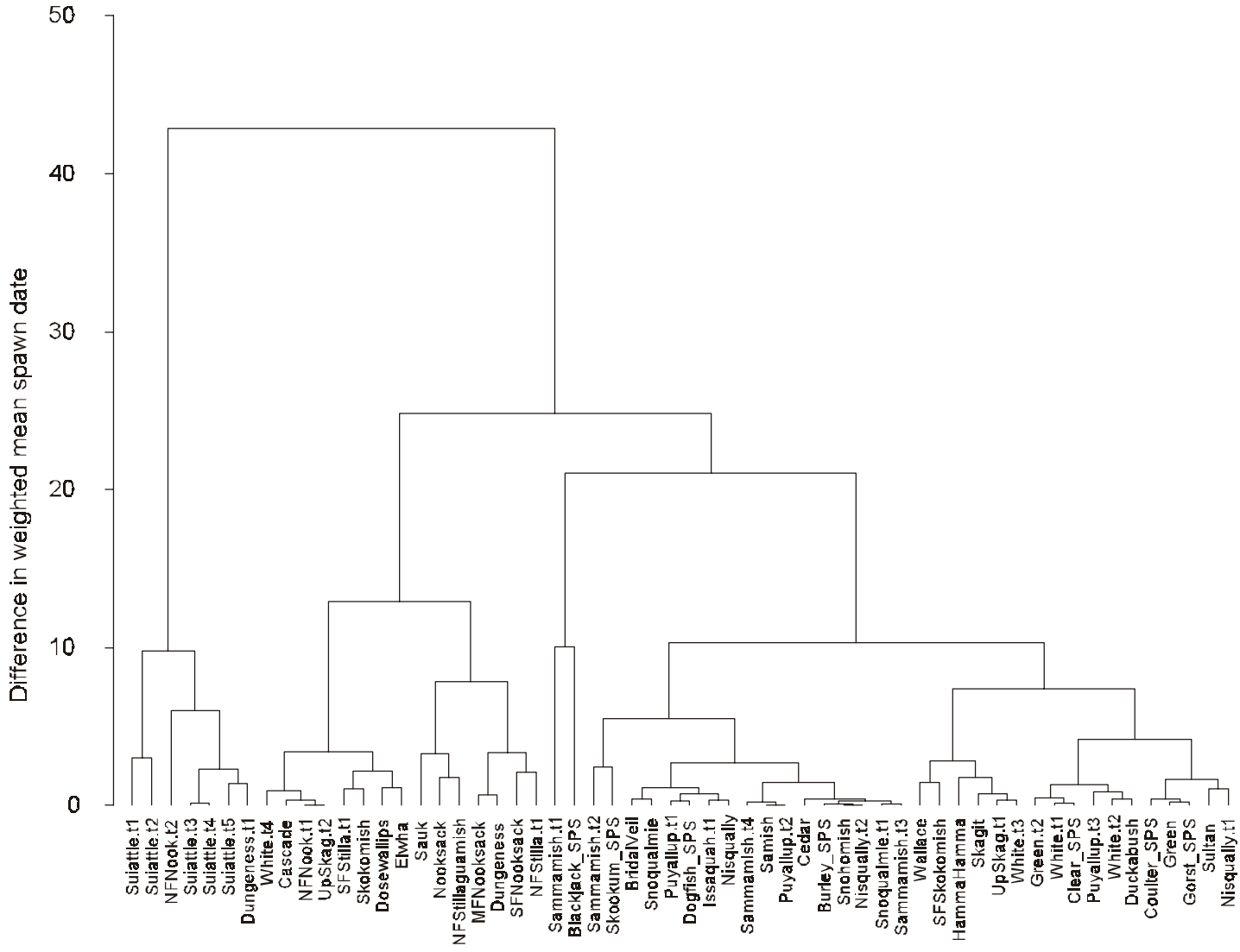

Figure 6. Clustering of Puget Sound chinook index survey areas based on weighted mean date of spawning. The mean date for each index area is calculated from the distribution of average relative densities of live spawners in annual index surveys. The absolute value of the difference between mean dates is the dissimilarity measure used in the UPGMA cluster analysis.

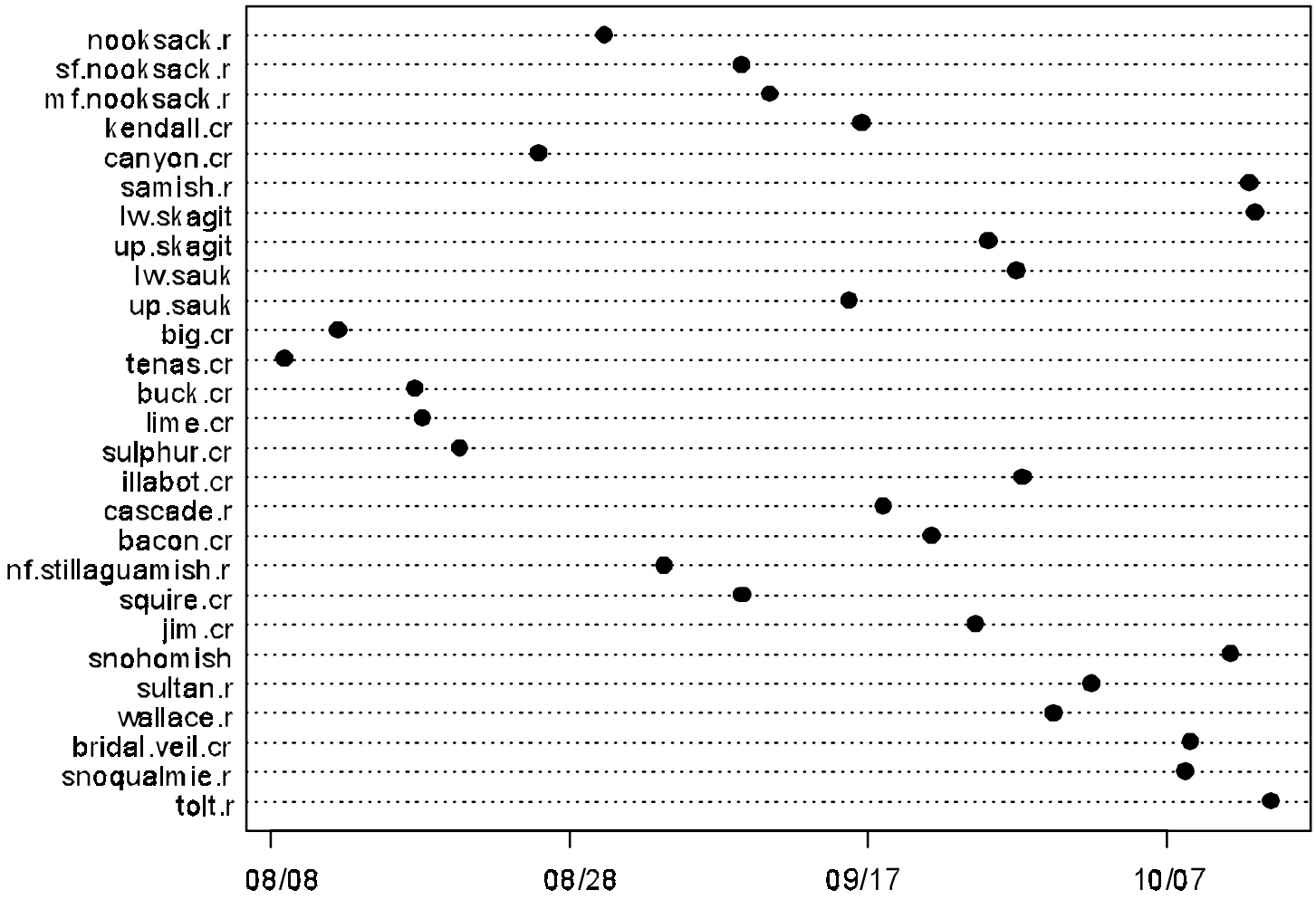

Figure 7. Weighted mean spawning dates for chinook in Puget Sound index survey areas. The mean date for each index area is based on the distribution of average relative densities of live spawners in annual index surveys. (A) North Puget Sound index areas. (B) South Puget Sound index areas.

B

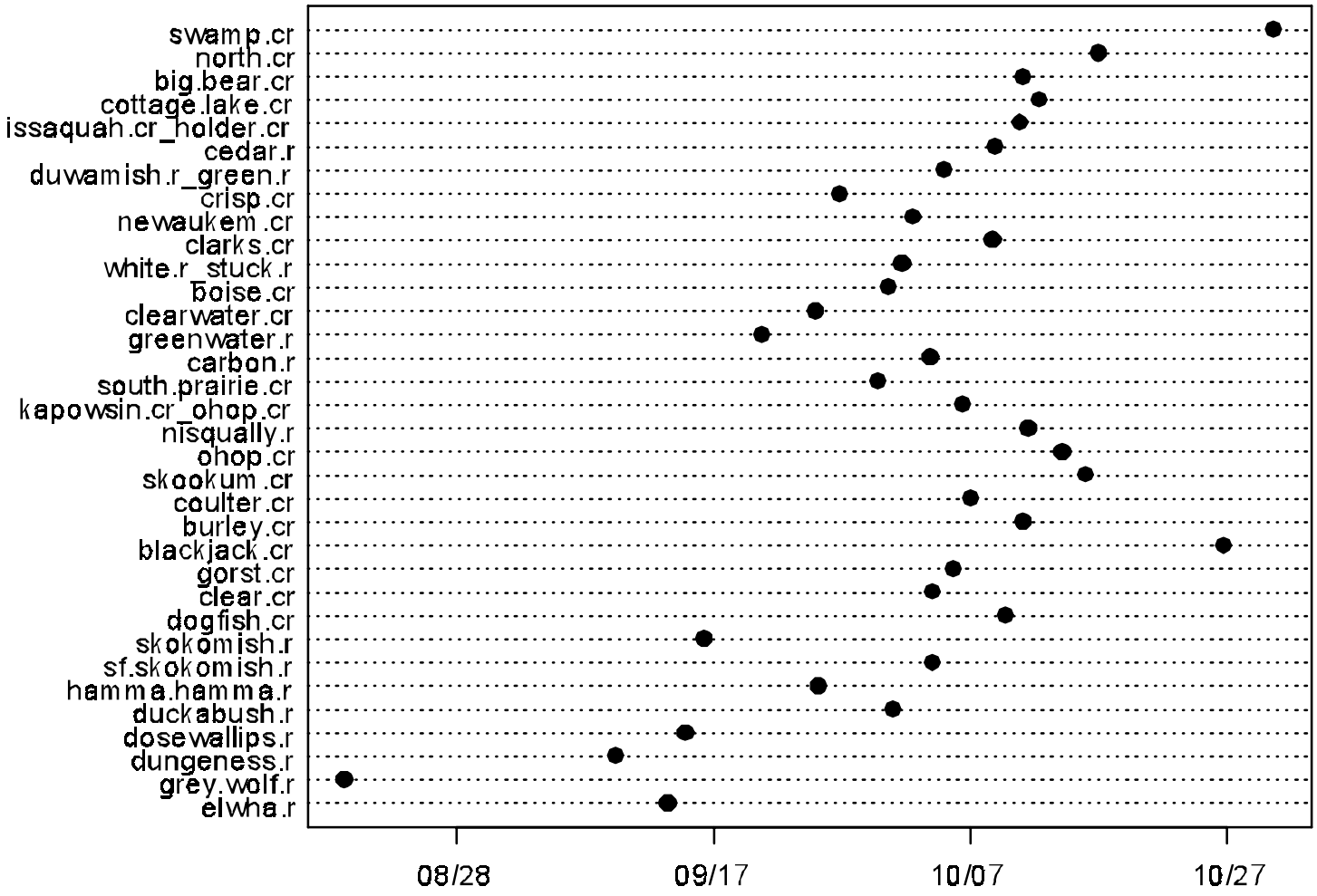

Figure 7 (Continued).

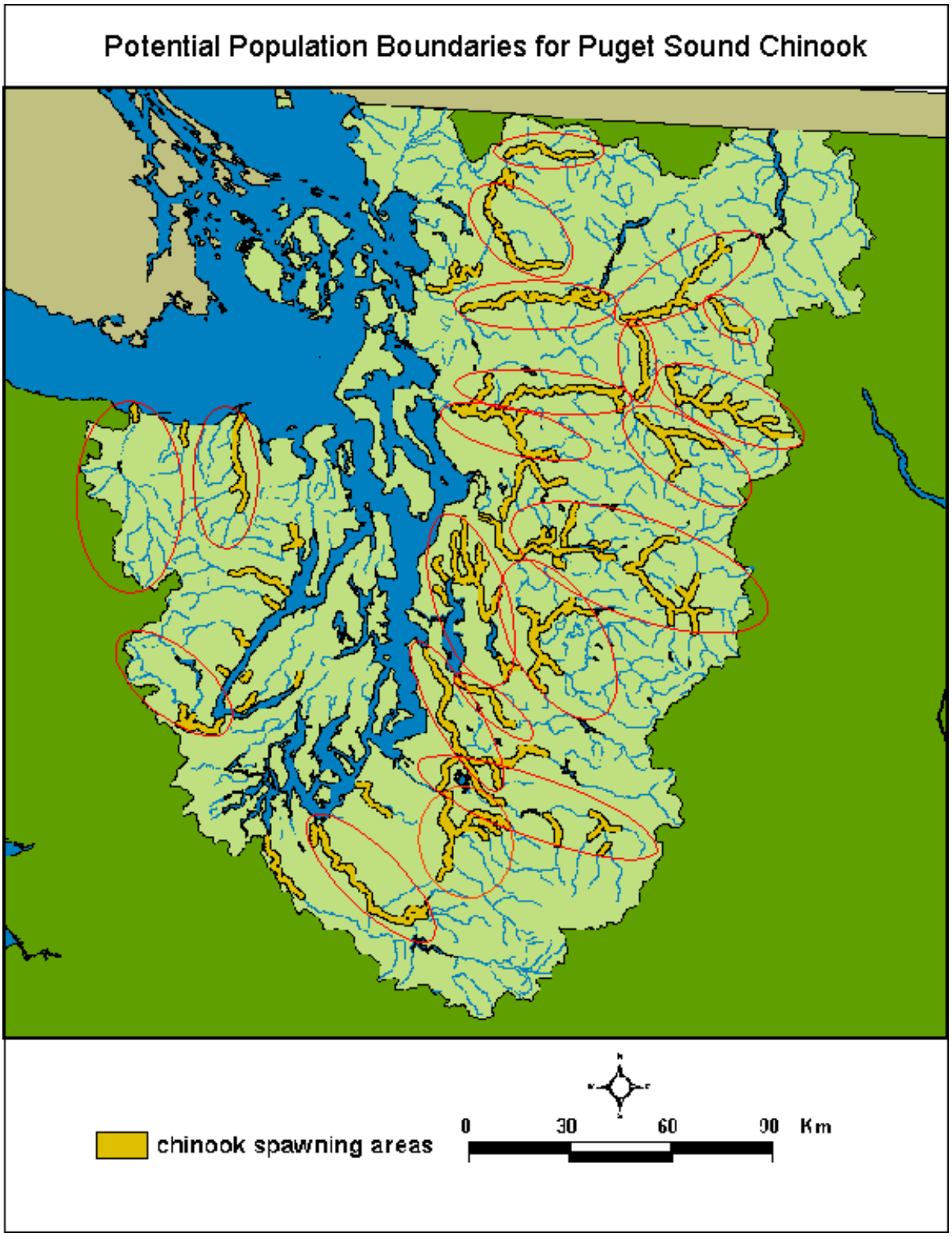

Figure 8. Proposed independent populations of chinook salmon in the Puget Sound ESU. Red ovals outline approximate geographic boundaries of watersheds containing historically independent populations of chinook salmon.